PATTERNS OF VEGETATION IN SOUTH-CENTRAL TASMANIA: A VIEW BASED ON PLANT MACROFOSSILS

By

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Statements and declarations

Declaration of Originality

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Giselle A. Astorga

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Abstract

Accumulations of plant macrofossils in lake sediments provide useful tools for identifying past local presence of plant species, community composition, and vegetation dynamics. However, plant macrofossils have rarely been used in the reconstruction of Lateglacial-Holocene vegetation changes in the Southern Hemisphere. Furthermore, such macrofossil studies are hampered by a scarcity of studies of taphonomic biases that may affect the final representation of plant species in sediments.

This thesis is the first systematic study of macrofossils covering an almost continuous stratigraphic sequence from the Lateglacial to the Holocene period (last 15,000 years) in southern Australia. Being located in a transitional climatic and vegetation zone near the treeline in south-central Tasmania, Lake Dobson is a lake formed in a glacial cirque which provides an ideal system to investigate both the taphonomy of Australian subalpine plants, and changes in vegetation and climate extending back to the Lateglacial.

The first component of the thesis is a taphonomic study comparing recently deposited leaf types from modern sediments of Lake Dobson with the vegetation surrounding the Lake. This study suggests that proximity of the plant community to the depositional site is critical for the representation of species in sediments. Additionally, the floristic composition of plant assemblages in sediments strongly agrees with the composition of species in vegetation near the lake. However, the number of leaves in sediments does not predict the same abundance of the species in the standing vegetation, mainly because of the large differences in leaf size and rate of

leaf production that exist among tree and shrub species. Overall, the results suggest that a correction factor accounting for proximity of the plant community to the site of deposition, differential leaf size, and number of leaves per ground area of vegetation produced by individual species can allow for better reconstruction of the original forest community.

The second component of the thesis analysed the floristic composition of plant macrofossils from a core drilled in the deepest part of Lake Dobson in south-central Tasmania, Australia. This study provides evidence of the role of local glacial survival versus the postglacial colonisation of plant species in the assembly of treeline communities during a period of acute environmental changes: the transition of the last glaciation to the modern Holocene environments. In particular, the presence of high subalpine/alpine plant species in the oldest macrofossil-bearing sediments in the Lake Dobson core strongly support the local survival —through at least the last part of the glacial— of poorly dispersed plant species such as species of alpine conifers, and the cool temperate tree *Nothofagus cunninghamii*. Additionally, this fossil record also provides evidence of the time lag in migration of *Eucalyptus* around the early middle-Holocene boundary. Thus, the current flora is best explained as having been assembled from a mixture of species that survived the glacial locally and species that migrated upslope after the climate amelioration in the Holocene. This study represents the first quantitative study of macrofossils in Australia for this significant period of environmental change.

The final chapter of the thesis explores the potential for anatomical aspects of leaf macrofossils to be used as indices of forest structure (in particular, closed forest versus open vegetation). In particular, it investigates the morphological and anatomical leaf variation of both fossil and contemporary leaves (i.e. canopy and litter leaves) of the cool temperate tree species *Nothofagus cunninghamii* from Lake Dobson. Overall, the results of this study suggest that allowing for the effects of leaf size and stomatal density in comparisons of vein density is a useful tool for reconstructing the structure of the vegetation from fossil leaves. In particular, it was found that closed canopy leaves have lower vein densities relative to stomatal density compared to open canopy leaves once differences in leaf size are taken into account. The fact that the relationship is dependent on leaf size and stomatal density is important because it means that canopy structure may be inferred from fossil leaves even when those leaves have undergone shrinkage in the process of fossilisation. However, the use of these parameters in the differentiation of open and closed litter it is not straightforward, and further research is required to clarify the higher upper to low canopy leaf representativity in the litter. This approach, however, represents an improvement on prior methods that directly employ vein density and have no capacity to allow for the effects of shrinkage.

The overall findings of this thesis have direct application to complement vegetation reconstructions by means of pollen analysis in southern temperate Australia. In particular, the study provides better understanding of taphonomic factors affecting the fossilisation of plant remains, and important implications to understand plant responses from a period of climate variability that is not yet well understood in the Southern Hemisphere: The transition from the Last Glacial to the modern Holocene environments.

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1 Chapter 1 – General Introduction

One important way of understanding how organisms respond to environmental change is to use fossil evidence to investigate how species in areas of steep ecological gradients have responded to dramatic and rapid environmental millennial-scale changes, such as those occurred from the transition of the last ice-age climates to the current interglacial conditions. This climatic transition occurred around 13–10 kyr ^{14}C BP (Hoek, 2008) caused a major reorganisation of the forest vegetation that has been intensively studied in temperate areas of the Northern Hemisphere using pollen records, and molecular tools (Birks 2003; 2009; Stewart et al. 2010; Williams 2009). However, pollen and molecular investigations have often provided conflicting evidence to explain the assemblage of plant communities after the ice retreat (i.e. rapid postglacial migration versus glacial refugia), and plant macrofossils may help to resolve such disparities (e.g. Birks, 2003; Stewart and Lister, 2001). In southern temperate regions phylogeographic studies based on DNA and pollen investigations have been used to answer such questions in southern temperate regions, although plant macrofossil studies are still sparse for this important period of environmental change in spite of the likelihood of good preservation of macrofossils from these ages.

The Last Glacial and post-glacial history of the vegetation from montane regions in southern latitudes has been mainly studied using fossil pollen extracted from sediment cores in lakes or bogs (Newnham et al. 2013; Newnham and Lowe 2000; Pugh and Shulmeister 2010). In New Zealand, for instance, most LGM studies (29–19 ka; Newnham et al. 2007) indicate widespread non-forest conditions with forest restricted mainly to refugial areas in the North Island during this period (McGlone et al. 2010). However, studies of pollen, beetles and chironomids have provided evidence of persisting woody vegetation in many areas across both North and South Islands (Burge and Shulmeister 2007; Marra and Leschen 2004; McGlone 1985; McGlone et al. 2010). Following the Last Glacial Maximum, New Zealand pollen records near the tree line indicate the initial upward podocarp forest expansion at c. 13 300 ^{14}C yr BP, and tree pollen types reaching maximum values at 13 000 ^{14}C yr BP. After this warming phase, the increase of cold-climate plants suggests a reversal at ca. 11 600–10 700 ^{14}C yr BP, but warmer conditions resumed at ca. 10 000 ^{14}C yr BP with the expansion of podocarp forest at lowland sites, and of montane-alpine forest at higher altitudes (McGlone and Basher 2012; Newnham and Lowe 2000).

In north-western Chilean Patagonia (40º–44ºS), pollen records supplemented with charcoal indicate cold and hyperhumid conditions with the dominance of *Nothofagus* parkland, Magellanic Moorland and conifers for the last part of the LGM between ~20–18 kcal BP (16 400–14 600 14C yr BP; Moreno and Leon 2003). After this period, pollen records indicate rapid deglacial warming conditions with abrupt increase of *Nothofagus dombeyi* at ~17.8 kcal yr BP leading to a rapid vegetation change with the expansion of the North Patagonian Forest at ca. 17.1 kcal BP and subsequent establishment of closed-canopy rainforest within by 16.8 kcal BP (Moreno et al. 2015). In southern Chile, the occurrence of a Younger Dryas event (YD) has been controversial (McCulloch et al. 2000) with some studies arguing for a homogeneous warming trend during the last glacial-Holocene transition (e.g. Bennett et al. 2000; Lamy et al. 2004; Markgraf 1991). However, there is also increasing evidence supporting a cold event close to the YD (Bertrand et al. 2008; Heusser et al. 1999; Moreno and Leon 2003; Moreno et al. 2001). Overall, during this period pollen studies record the decline of thermophilous species and re-expansion of cold resistant taxa (i.e. *Podocarpus nubigena* and *Nothofagus dombeyi*-type). Following, pollen records provide evidence of an early Holocene climatic optimum (~ 10.5–7.5 kcal BP) interpreted as dry and warm, and recording the expansion of thermophilous tree species (i.e. *Eucryphia cordifolia*, *Caldcluvia paniculata*, *Lomatia*/*Gevuina* and Myrtaceae) and the decline of *Podocarpus* (Abarzúa et al. 2004; Moreno and Leon 2003; Moreno et al. 2001).

Similarly, most Last Glacial Maximum pollen investigations (LGM: 24 000–18 000 years ago; Colhoun and Shimeld 2012) in south-eastern Australia, and particularly Tasmania, indicate the ubiquitous presence of alpine grassland and herbfields at low to mid-altitude sites (Colhoun 2000; Colhoun et al. 1999; Colhoun and Shimeld 2012; Colhoun and Van De Geer 1986b). These pollen assemblages have indicated a treeline depression and temperature drop of 3–8°C during the LGM (Colhoun 1985; Fletcher and Thomas 2010; McKenzie 1997; McKenzie and Kershaw 2000). However, phylogeographic studies based on DNA provide evidence for the survival of a suite of species in areas that pollen vegetation reconstructions suggest had environments inconsistent with the current environmental ranges of these species. In particular, molecular studies strongly support the idea that many important plant taxa survived the LGM in multiple glacial refugia across Tasmania (McKinnon et al. 2004; McKinnon et al. 2001; Nevill et al. 2008; Nevill et al. 2010; Worth et al. 2010; Worth et al. 2009). Additionally, these studies suggest that tree species have shown very low mobility and often survived in areas that would be unexpected based on their modern bioclimatic ranges and current understanding of Last Glacial environments (Worth et al. 2014; Worth et al. 2009). These conflicts between molecular and paleoclimatic evidence can best be explained by the species occurring in climates that are outside their current bioclimatic ranges (Worth et al. 2014).

Plant macrofossils can assist pollen and molecular vegetation studies, mainly because they can provide direct evidence of the presence of a taxon in the local paleovegetation (Birks 2007; Birks and Birks 1980; Dieffenbacher-Krall 2007; Huntley 1996; Jackson and Booth 2007; McQueen 1969). In particular, well-preserved macrofossils can be identified to finer taxonomic levels (often to species level), whereas pollen is often identifiable to generic or family level. Furthermore, plant macrofossils are typically transported short distances (10 to100 metres except where there is transport by major streams), unlike many pollen types that can be transported hundreds or even thousands of metres (Birks and Birks 1980; Jackson and Booth 2007). Additionally, it is widely recognised that the capacity of pollen studies to provide information of plant community dynamics in treeless situations (e.g. alpine late-glacial landscapes), or determining the past position of the treeline and glacial refugia is quite limited (Barnekow 1999; Bennett et al. 1991; Birks and Birks 2008; Birks and Birks 2000). Thus, plant macrofossils may provide insights into ecological processes and related climate conditions that cannot be obtained from other currently available methods (Birks 2001; Birks 2007; Birks and Birks 2006; Birks and Birks 1980; Dieffenbacher-Krall 2007; Huntley 2001). However, past vegetation studies based on the use of disarticulated plant structures need to take into consideration the specific taphonomic factors affecting the potential for fossilisation of individual species and different plant organs.

Tasmania (40–43°S and 144–149°E), in southernmost temperate Australia, is a study area of central importance for understanding the environmental changes that occurred as a consequence of the late Quaternary mid-latitude glaciations in the Southern Hemisphere (Barrows et al. 2001). In particular, Tasmania is ideally located to record environmental changes as it lies under the direct influence of the South Westerly

Winds and other large-scale ocean-atmosphere climate drivers that interact in the region —i.e. El Niño Southern Oscillation, Southern Annular Mode, the Subtropical Ridge, and the Indian Ocean Dipole— (Abram et al. 2009; Gagan et al. 2004; Gillett et al. 2006; Hendon et al. 2007; Petherick et al. 2013; Prowse and Brook 2011). The island is also one of the few mid-latitude areas in the Southern Hemisphere that were glaciated during the late Quaternary. In particular, there is evidence for at least three episodes of glaciation preceding the Last Glacial in Tasmania (Colhoun and Fitszimons 1996; Colhoun et al. 1996; Mackintosh et al. 2006). The Last Glacial resulted in much less extensive glaciation than some previous glaciations in Tasmania with ice extent mainly limited to areas of the West Coast Range, parts of the Central Plateau and other high plateau areas (Colhoun 2002; Colhoun et al. 1996). However, it is unclear whether this lesser extent of ice was due to smaller temperature depression, or greater aridity during the LGM compared to previous glacial periods with more extensive ice conditions (Colhoun and van De Geer 1998; Petherick et al. 2013 and references therein). Additionally, it is not clear whether the LGM imposed greater or lesser stresses on forest vegetation than earlier glacial stages.

Lake Dobson in Mount Field National Park, south-central Tasmania provides an ideal opportunity to investigate the role of local glacial survival versus the postglacial colonisation of plant species in the assembly of treelines at the Last Glacial-Interglacial Transition. Thus, Mount Field National Park is located between two distinctive climatic and vegetation systems. To the west of the park there is a perhumid region dominated mainly by sedgeland interspersed with areas of forest including cool temperate forest dominated by *Nothofagus cunninghamii*. To the east a subhumid region of open forests dominated by *Eucalyptus* (Jackson 1999; Macphail 1979, 1984; Ogden and Powell 1979). In addition, the park contains alpine and subalpine areas with numerous glacial lakes and tarns, the sediments on the bottom of which may provide pollen and macrofossils records documenting vegetation changes in the region since the Last Glacial (Mackintosh et al. 2006; Macphail 1979).

1.1 Thesis structure and research objectives

This thesis presents three different studies written in journal manuscript style that collectively demonstrate the value of using plant macrofossils as a tool to assist late Quaternary vegetation reconstructions in southern Australia. Although there have been a number of studies of macrofossils from the late Quaternary in southern Australia especially in Tasmania (Bresnehan 1993; Colhoun et al. 1993; Colhoun et al. 1989; Fitzsimons et al. 1990; Gibson et al. 1987; Jordan et al. 1991; Rowell et al. 2001), they represent studies of isolated assemblages of macrofossils (i.e. "snapshots" in time) and generally predate the Last Glacial Maximum. This thesis is therefore the first systematic study of macrofossils covering an almost continuous stratigraphic sequence from the Lateglacial to the Holocene period (last 15,000 years).

Chapter 2 begins by presenting the analysis of plant macrofossils from surface sediment samples of Lake Dobson. This study investigates the modern taphonomy of Australian subalpine/alpine plants, and focuses on the identification of key factors affecting the final representation of plant macro-remains in sediments. It also presents an intrinsic representativity index that indicates the bias against preservation of a species due to the cost of transport and decay. This representativity index has the potential to provide a more accurate picture of the relationship of abundance between leaves assemblages in sediments and their source vegetation. This study provides a sound taphonomic basis for interpreting macrofossil studies of the same lake (Chapters 3 and 4).

Chapter 3 focuses on the stratigraphic analysis of plant macrofossil assemblages from a long sediment core from Lake Dobson. This study spans last ~15 000 years, representing the transition from the Lateglacial to interglacial conditions, and aims to reconstruct the postglacial reorganisation of subalpine plant communities as a response to environmental changes in temperature, precipitation, and fire activity. It presents a synthetic temperature variable constructed by PCA using regional and local temperature records. Multivariate gradient analysis (CCA) is used to detect species-environment relationship. Overall, this study presents plant macrofossil evidence of differential plant responses to environmental change. In particular, it provides evidence for the local glacial survival of some high subalpine/alpine plant species, and the time lag migration of *Eucalyptus* establishing in the area around the early to mid-Holocene transition.

In chapter 4, a methodology that explores the potential of leaf macrofossils to identify past forest structure is presented. In doing so, variation in anatomical and morphology leaf traits (i.e. leaf area, vein density and stomatal density) from contemporary canopy and litter leaves of *Nothofagus cunninghamii* are used to discriminate between open and closed vegetation. Results of this study indicate that while is possible to differentiate between open and closed canopy forest from foliage leaves, the discrimination of forest structure from litter is precluded by the higher sun to shade leaf representativity. This study also highlights the need for further research to understanding the modern relationship between leaf parameters and forest structure that is required to refine paleoclimatic interpretations based on leaf characteristics.

2 Chapter 2 – Towards understanding the fossil record better: Insights from recently deposited lake macrofossils in Australia

2.1 Abstract

Accumulations of plant macrofossils in lake sediments are increasingly being used to refine our understanding of past vegetation history, ecological processes and related climate conditions in late Quaternary reconstructions. However, past vegetation studies based on the use of disarticulated plant structures need to consider taphonomy (i.e. the specific potential for fossilisation of different species and different plant organs).

Taphonomic studies can help understand both the potential for fossilisation of individual taxa and the effects of specific intrinsic factors, such as the size and weight of organs, in the final representation of plant species in depositional settings. This study investigated the potential source vegetation of plant remains from modern sediments extracted from a small subalpine lake in southern Tasmania, Australia to provide understanding of the taphonomic factors affecting the final representation of plant species in sediments.

It was found that the distance of the plant community to the site of deposition is an effective filter in determining the representation of plant parts in the sediments of Lake Dobson. Thus, leaf assemblages are mainly derived from areas of vegetation close to the lake; although leaf counts fail to predict the same relative abundance of species in the source vegetation mainly because of the big differences in leaf size and rate of leaf production among species. In particular, small-leaved shrub species such

as many members of Ericaceae, produce comparatively many more leaves and tend to be over-represented in sediments. In contrast, large-leaved tree species that are dominant in the standing vegetation (e.g. *Eucalyptus*) are under-represented in sediments mainly because they produce substantially fewer foliar organs per ground area of vegetation.

The intrinsic representativity index developed in this study indicates the bias against preservation of a species due to the cost of transport and decay, and provides a more accurate picture of the relationship of abundance between leaf assemblages in sediments and their source vegetation. Understanding these biases may have important implications for the interpretation of the fossil record.

2.2 Introduction

Accumulations of plant macrofossils in lake sediments are increasingly being used to refine our understanding of past vegetation history, ecological processes and related climate conditions (Allen and Huntley 1999; Birks 2001; Birks 2007; Birks and Birks 2006; Birks and Birks 1980; Huntley 2001). Plant macrofossils may provide information complementary to that derived from the analysis of pollen grains and spores (Birks 2001; Birks 2007; Boyce 2008; Jackson and Booth 2007). However, plant fossil assemblages can only be validly interpreted in the light of the potential biases resulting from the differential preservation of different species. Plant taphonomy is the discipline investigating such potential for fossilisation (Ferguson 2005; Gastaldo 1987; Gastaldo 1990; Spicer 1989).

The potential for fossilisation of plant parts may vary depending on both inherent characteristics of plants organs —hereinafter referred as intrinsic factors— and extrinsic factors such as features of the depositional environment (Martin 1999b; Spicer 1991). In particular, intrinsic characteristics of plant organs can be major determinants of the likelihood of a species becoming fossilised. For example, the rate of leaf production and size, among other characteristics, can affect the capacity of plant organs to be transported and represented in sediments (Ferguson 2005; Spicer 1989; Spicer 1991). However, the potential for fossilisation is also affected by extrinsic factors, especially by topographic features of the depositional environment, the geographic distance of plant communities to the potential site of deposition, and the presence and ability of wind and/or flowing water to transport plant materials to the site of deposition (Ferguson 1985; Ferguson 2005; Gastaldo and Demko 2011; Greenwood 1991a; Spicer 1989; Spicer and Wolfe 1987). Thus, complex interactions of intrinsic and extrinsic factors may play a key role in the final representation of plant parts within sediments. As a result, fossil assemblages rarely reflect their source vegetation in simple one to one relationships of abundance (Birks 2001; Birks 2007; Birks and Birks 1980; Spicer 1991; Spicer and Wolfe 1987). Reconstructions of past plant communities may therefore benefit from a better understanding of the specific potential for fossilisation of different species and different types of plant organs.

The analysis of plant macrofossils from surface sediments, the uppermost recently deposited sediments in depositional environments such as lakes, can enhance the understanding of taphonomic processes (Dieffenbacher-Krall 2007; Spicer and Wolfe 1987; Warner 1988). These studies can provide insights into the relationship of abundance of organs from a specific taxon present in the sediments, and the frequency of the same taxon in the source vegetation (Birks 2007; Spicer and Wolfe 1987). In these studies, however, the representativity of any given species may vary markedly depending on the system in which it is measured. This is mainly because the representativity is a proportion of all the organs preserved, and is therefore non-independent of the other represented species. Thus, a more powerful approach is to use taphonomic studies to develop an understanding of the effects of individual intrinsic factors in the final representation of plant organs in depositional settings, such as those determining the rates of production, shedding, and decay of individual organs.

Studies in terrestrial and aquatic systems in Europe (Allen and Huntley 1999; Birks and Birks 1980; Collison 1983; Greatrex 1983; Spicer 1981) and North America (Demko et al. 1998; Dieffenbacher-Krall and Halteman 2000; Dunwiddie 1987;

Spicer and Wolfe 1987) have identified some general taphonomic patterns, although large differences between systems and geographic locations also exist.

Such studies suggest firstly that plant macrofossils are not usually dispersed long distances from their source vegetation. Consequently, plant macrofossil assemblages tend to reflect the local vegetation with plants growing in distant communities being poorly represented in sediments (Birks 2001; Birks 2007; Birks and Birks 1980; Gastaldo et al. 1996; McQueen 1969; Rich 1989; Rowell et al. 2001; Spicer and Wolfe 1987). Additionally, locally derived leaf assemblages can be characterised by the presence of well preserved, complete or nearly complete leaves, whereas allochthonous deposits tend to be mainly composed by highly fragmented leaves in poor state of preservation (Gastaldo et al. 1996). Moreover, intrinsic characteristics such as rate of leaf production, weight, size and chemical composition of plant organs can affect the final representation of plant macrofossils within sediments (Birks and Birks 1980; Ferguson 1985; Greenwood 1991b; Rich 1989; Spicer 1981; Spicer 1991). Thus, plants producing robust leaves (e.g. high leaf mass per unit area: LMA), or plants species producing small and high numbers of leaves per unit area of ground cover are expected to be strongly represented in sediments (Steart et al. 2005). This assumption suggests that taxonomic groups containing these plant traits may be better represented than others in sediments (Cornwell et al. 2008; Wright and Cannon 2001; Wright et al. 2005). Additionally, taphonomic studies to date have shown that the composition of species in the standing vegetation mirror to that present in forest litter or sediments, although the relative contribution of each dominant species can be distorted (Schimanski and Bergstrom 1998). Moreover, several taphonomic studies have established that leaf counts fail to predict the abundance of species in the standing vegetation especially if there are large differences in leaf size, in which case leaf area may better reflects the patterns of species dominance (Burnham et al. 1993; Collison 1983; Drake and Burrows 1980; Hill and Gibson 1986; Spicer and Wolfe 1987; Steart et al. 2005). Consequently, it can be expected that common species in the standing vegetation and forest-litter will be also common within the sediment samples although reconstructions may be potentially biased towards species producing small and higher number of leaves.

In contrast to Northern Hemisphere systems, few taphonomic studies have been undertaken in southern temperate areas. Most of them have studied forest floor litter or accumulations of leaves on river banks and beds (Carpenter and Horwitz 1988; Steart et al. 2006; Steart et al. 2005), but only a handful have investigated lacustrine environments (Drake and Burrows 1980; Hill and Gibson 1986). There are several reasons to suspect that the taphonomy of temperate Southern Hemisphere systems may differ from systems in northern latitudes. For instance, the floras of these regions have much higher proportions of evergreen species compared to deciduous species than northern temperate systems (Box 2002; Jordan 2011; McGlone et al. 2004). Austral temperate floras also have a high diversity and abundance of microphyllous and sclerophyllous species such as those in the families Nothofagaceae, Myrtaceae, and Proteaceae, and also distinct lineages within more widespread families such as Asteraceae, Rutaceae, Ericaceae, Poaceae and Fabaceae (Hill and Orchard 1999).

This study investigates the taphonomy of Australian subalpine plants in the area of Lake Dobson, south-central Tasmania by combining the information provided by plant macroremains collected by Hill and Gibson (1986) with information of present day-vegetation community data from the surrounding area. Although Hill and Gibson

(1986) made extensive macrofossil collections, they made no analyses of reproductive structures or detailed consideration of the potential source vegetation. This study aims to elucidate the modern representation of plant macrofossils within the sediments of Lake Dobson, and the specific relationship of the plant remains with the standing vegetation in the catchment. Specifically, it focuses on the identification of taphonomic factors affecting the final representation of plant species within sediments, and whether the observed patterns are similar to those found in other systems and geographic areas.

2.3 Materials and methods

2.3.1 Study site

Lake Dobson (42° 41.019’ S, 146°35.478’ E) is located in the sub-alpine area of Mt. Field National Park, south-central Tasmania at an altitude of 1034 m (Bradbury 1986; Macphail 1979; Ogden and Powell 1979; Weatherley and Nicholls 1955). The lake covers *c*. 5.7 ha, and occupies a glacial cirque bounded on the west part by a headwall 250 m high rising at a slope of ~30°, and on the eastern side by a lateral moraine (Fig. 2-1). The lake is irrigated mainly by two incoming streams: The Golden Stairs Creek flowing from the Mawson Plateau down to the east, and Eagle Tarn Creek connecting Lake Dobson with Eagle Tarn to the north (Fig. 2-1). Prevailing winds in Lake Dobson area blow predominantly from west to east (Hill and Gibson 1986).

The climate of the region is cool temperate in overall character, and transitional between a perhumid region of wet vegetation types including extensive wet sedgeland/heaths and cool temperate closed forests, extending to the west, and a subhumid region of *Eucalyptus* open forests and grasslands extending to the east (Harris and Kitchener 2005; Macphail 1979; Read 1999). Climatic parameters generated by the climatic prediction program BIOCLIM (Houlder et al. 2003) indicate that annual mean temperature at Lake Dobson is 6.2°C, mean temperatures of the warmest and coldest quarter are 10.3°C and 2.3°C, respectively and annual mean precipitation is 1454 mm. Snowfalls are common between July and September.

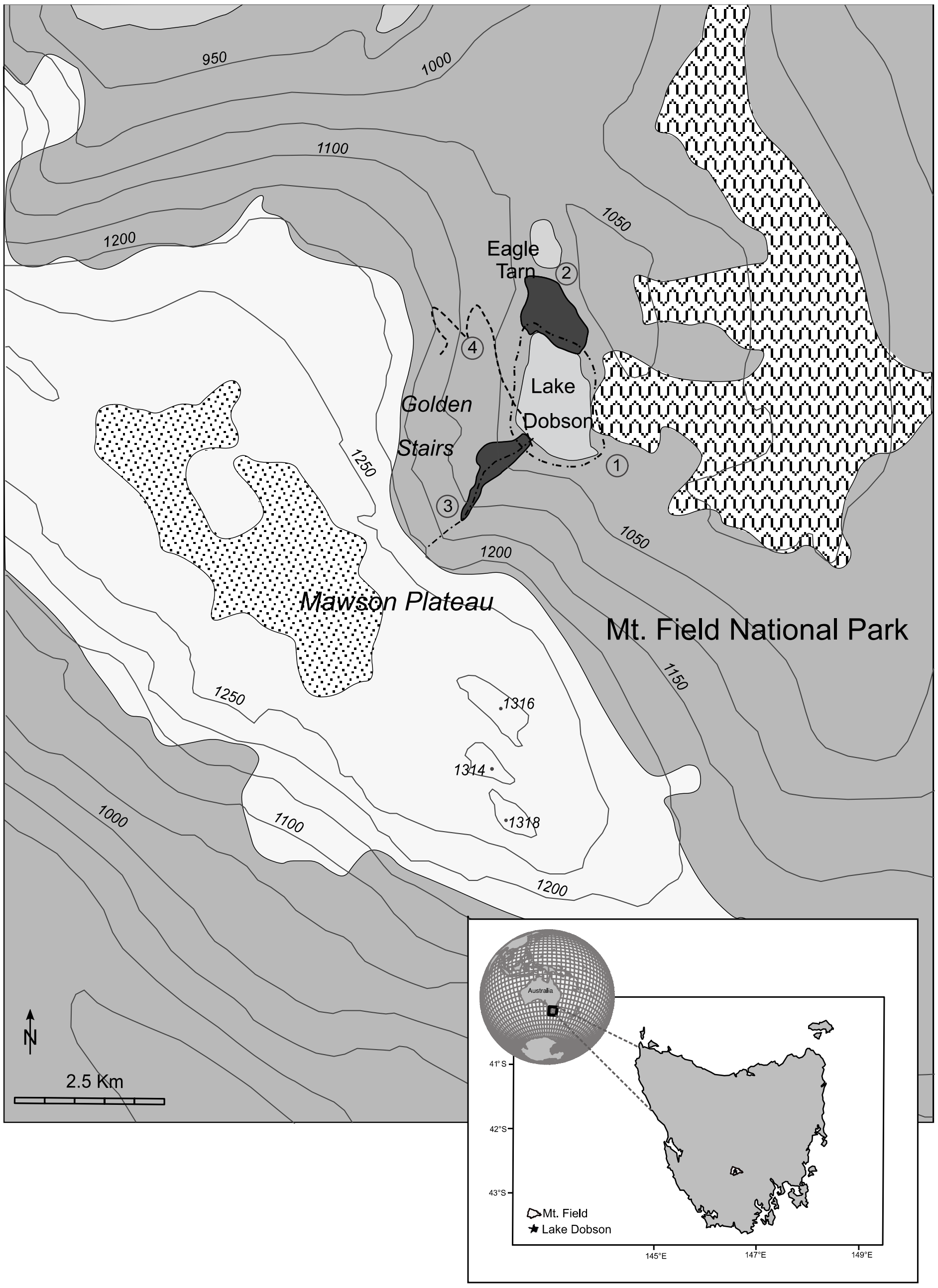

Figure 2-1 Location of Lake Dobson in Mount Field National Park, south-central Tasmania, Australia. Vegetation types present in the catchment as follow: pale grey = alpine heath; stippled = alpine moorland; medium grey = *Eucalyptus* woodland; dark grey = Mountain rain forest (dominated by *Nothofagus cunninghamii*); and waves = subalpine moorland (button grass). Numbers and dashed lines indicate the surveyed areas of vegetation: 1) Lakeside vegetation, 2) Eagle Tarn Creek vegetation, 3) Golden Stairs Creek vegetation, and 4) upper catchment vegetation.

2.3.2 Present day vegetation and surveys

The areas near Lake Dobson (Fig. 2-1) form a mosaic of woodlands, heaths, and sedgelands. The heaths are mainly dominated by species of the Ericaceae, Myrtaceae, Proteaceae and Asteraceae families, while the sedgeland vegetation is dominated by members of the Cyperaceae, Restionaceae, Asteliaceae and Gleicheniaceae families (Crowden 1999; Harris and Kitchener 2005). The subalpine vegetation is characterised by woodlands dominated by *Eucalyptus coccifera* and *Eucalyptus subcrenulata* interspersed with stands of montane rainforest dominated by *Nothofagus cunninghamii* (Nothofagaceae) or the endemic conifer *Athrotaxis cupressoides* from the Cupressaceae family (Kirkpatrick 1982). Alpine vegetation (i.e. above the altitudinal tree line) occurs ~ 1220 m of altitude, and is mainly composed of a mosaic of sedgeland, herbfield (including cushion plants), sclerophyll heaths and patches of dwarf coniferous species including the endemic conifers *Diselma archeri*, *Pherosphaera hookeriana* and *Microcachrys tetragona,* and *Podocarpus lawrencei* (Crowden 1999; Harris and Kitchener 2005; Kirkpatrick 1982).

In this study, the hydraulic catchment of Lake Dobson is assumed to represent the potential catchment for the leaves, flowers, and fruit found in sediments (Fig. 2-1). Four areas of vegetation within the catchment were surveyed in 99 sample quadrats, and the composition and the relative abundance (% ground cover) of vascular species recorded. Percentages of ground cover where transformed to squared meters of ground cover (m^2) when necessary. The areas of vegetation were chosen to test whether the distance of plant communities to the site of deposition, and the presence of transport mechanisms in association to these vegetation areas, such as flowing water, may better explain the origin of plant assemblages incorporated within Lake Dobson sediments. These areas were: Lakeside vegetation (58 x 10 m^2 quadrat plots), defined as the standing vegetation immediately surrounding the lake in a five metres width band. Vegetation values for this area were adjusted to allow for foliage overhanging the lake, so some overhanging species may have covers greater than 100%. Two areas of riparian vegetation located along the two main inflowing streams to the lake; Golden Stairs Creek (20 plots of 25 m^2) and Eagle Tarn Creek vegetation (10 plots of 25 m^2). Upper catchment vegetation (11 plots of 25 m^2) represents vegetation growing in areas at or above the local treeline. This latter area represents typical vegetation of the upper catchment. Additionally, litter samples from the forest floor of the lakeside vegetation were taken in a transect line at 50 m intervals, and the plant material from twenty-one quadrat plots (0.84 m^2) was collected. This material was sorted and the composition and abundance of species recorded. For a detailed composition of species in the areas of vegetation and litter included in this study, see Appendix 1.

2.3.3 Surface sediment samples

One hundred and fifty-three surface sediment samples from Lake Dobson collected by Hill and Gibson (1986) were re-assessed. These samples were collected from three transects positioned at 10 m intervals across the centre of the lake running parallel to the direction of the prevailing winds (see Hill and Gibson 1986 for more details). The plant material was reassessed under a stereomicroscope at 10–40x magnifications. Taxonomical identifications to species level were made whenever possible by comparison with plant reference collections held at the School of Plant Science, University of Tasmania, and taxonomic plant descriptions published by Curtis (1963;

1967), Curtis and Morris (1975; 1979; 1994), Stevens *et al* (2004), and Weiller (1996; 1999).

2.3.4 *Leaf traits and indices of species representation*

For each of the most common species within the lake sediments and standing vegetation (Table 2-3), leaf area, leaf area index, number of leaves per unit of ground area and leaf mass per area (LMA) were calculated in order to investigate whether these traits can explain the composition and abundance of plant macro-remains found within the sediments of Lake Dobson.

Leaf dry mass per area (LMA g m^{-2}) of modern species was determined following the protocol of Cornelissen *et al*. (2003). The leaf area of 20 fully exposed sunlight leaves, including petioles, from five individuals per species were measured using a flatbed scanner at a resolution of 1200 dpi, and the image analysis software IMAGEJ. After area determinations, the plant material was oven-dried at 60 °C for 72 hrs. LMA was then calculated by dividing leaf dry mass by leaf area of the fresh material. In order to determine the number of leaves per area of vegetation for each of the most common species, the leaf area index was calculated. The leaf area index (LAI m^2/m^2) defined as one half of the total leaf area per unit ground surface area (Jonckheere et al. 2004) was estimated using the harvesting method. Destructive samples for three individuals per species were taken removing the total number of green leaves enclosed in a specific harvested area. Then, LAI was calculated by dividing the total dry mass of leaves present in the harvested area by LMA according with the methodology described by Bréda (2003). Finally, the number of leaves per unit area of vegetation was obtained by multiplying the percentage of cover abundance of every species (in each of the four areas of vegetation) by their LAI divided by the corresponding mean leaf area of the species. The number of leaves per unit of ground area was then used to calculate the intrinsic representativity for each of the most common species represented in sediments (equations a and b).

$$\text{No. leaves per area of vegetation} = \frac{\text{LAI } (m^2/m^2)}{\text{Mean leaf area } (m^2)} \text{ x harvested area } (m^2) \qquad \text{(a)}$$

$$\text{Intrinsic representativity} = \frac{\text{No. leaves in sediments}}{\text{No. leaves per area of vegetation}} \qquad \text{(b)}$$

The apparent representativity index for each of the most common species was calculated by dividing the abundance of leaves of each species in sediments by the abundance (% of ground cover expressed in m^2) of that species in the vegetation. Representativity indices were calculated for each of the four areas of vegetation.

2.3.5 Agreement between plant macro-remains and standing vegetation

The strength of the association between the relative abundance of each taxon within the lake sediment, the areas of vegetation, litter samples, and leaf traits was measured using Spearman rank-order correlations (Sokal and Rohlf 1995). Specifically, rank-order correlations were used to assess whether relative abundance of species represented in the plant macrofossils assemblages and the relative abundance of the same species in the standing vegetation ranked in equal or opposite numerical abundance.

The same procedure was used to assess whether per leaf area representation (number of subfossil leaves multiplied by the leaf area of the same modern species), and number of leaves per ground area of vegetation can better predict the observed patterns of species abundance when compared with leaf counts. Additionally, the average leaf size of the species most commonly represented in the forest litter of the lakeside vegetation and leaf assemblages was investigated using a one-way ANOVA. All analyses were performed using the R package *Rcmdr* (Fox 2007).

2.4 Results

2.4.1 Composition of the plant macrofossil assemblages

Approximately 28,000 identifiable macroscopic plant remains were recovered from the 153 surface sediment samples of Lake Dobson (Table 2-1). The number of plant remains per sample ranged from 2 to 1403, with a mean of 182 ± 245 (± SD) and a median of 105. All leaf types were identified, although 138 (4%) reproductive structures remained unidentified.

Diverse plant groups including conifers, ferns, and dicotyledonous and monocotyledonous angiosperms were identified. Altogether, leaves and reproductive structures revealed the presence of 45 species from 18 families. The combination of leaves and reproductive structures increased the taxonomic resolution, especially because leaves failed to record herbs and monocotyledons, and reproductive organs lacked records of conifers (Table 2-1; Fig. 2-2). Thus, reproductive structures report 15 species not recorded as leaves, leaves document 16 species not recorded as reproductive organs, whereas only 14 species were recorded as both (Table 2-1; Fig. 2-3).

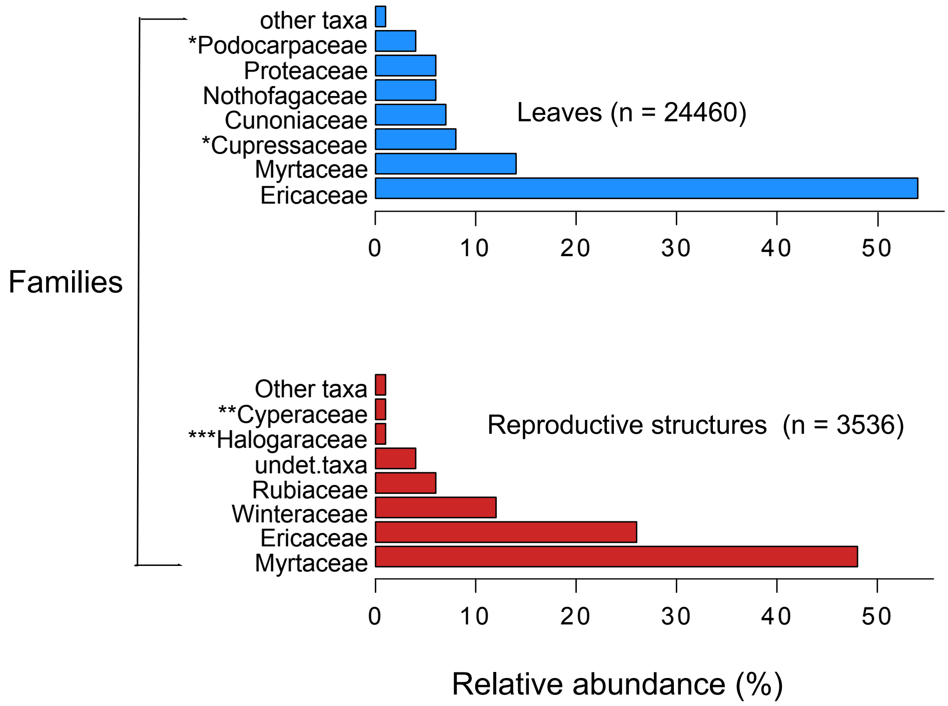

Figure 2-2 Representation by family for reproductive structures and leaves found in surface sediment samples from Lake Dobson (*conifers; ** monocotyledonous; *** dicotyledonous herbs).

Common tree and shrub species in closer areas of vegetation to the lake were well represented in sediments. For instance, common in both macrofossil assemblages and standing vegetation were *Eucalyptus coccifera, Nothofagus cunninghamii*, *Epacris serpyllifolia*, and the conifers *Athrotaxis cupressoides* and *Pherosphaera hookeriana*. In contrast, rare species in the standing vegetation and forest litter such as *Gahnia grandis*, *Carpha alpina*, *Gonocarpus montanus*, and *Phyllocladus aspleniifolius* were equally rare in the lake sediments.

In particular, leaf assemblages provided evidence of the presence of 30 plant species within ten families (Table 2-1). Overall, leaf assemblages were dominated by species of shrubs producing small and high number leaves, whereas trees species producing bigger leaves were underrepresented in sediments. The twelve most abundant species among leaf assemblages accounted for 96% of the total number of leaves. *Epacris serpyllifolia*, a shrub from Ericaceae, dominated the leaf counts, contributing with 50% of the total number of leaves. Other well-represented species were the conifer *Athrotaxis cupressoides* (9%), *Leptospermum lanigerum/rupestre* (8%), *N. cunninghamii* (7%), and *Bauera rubioides* (6%), (Table 2-1). Additionally, leaf assemblages recorded the presence of seven other conifer species from Podocarpaceae and Cupressaceae, the fern *Gleichenia alpina*, and three species from Proteaceae (Fig. 2-3). These species were absent from the assemblages of reproductive structures, with the exceptions of *Athrotaxis cupressoides* and *Orites revolutus* that were marginally represented (Table 2-1).

The identification of reproductive structures revealed the presence of 28 species among 15 families (Fig. 2-3). Three types of reproductive structure remained with uncertain taxonomic status after the analysis, while one type was only identified to the family level.

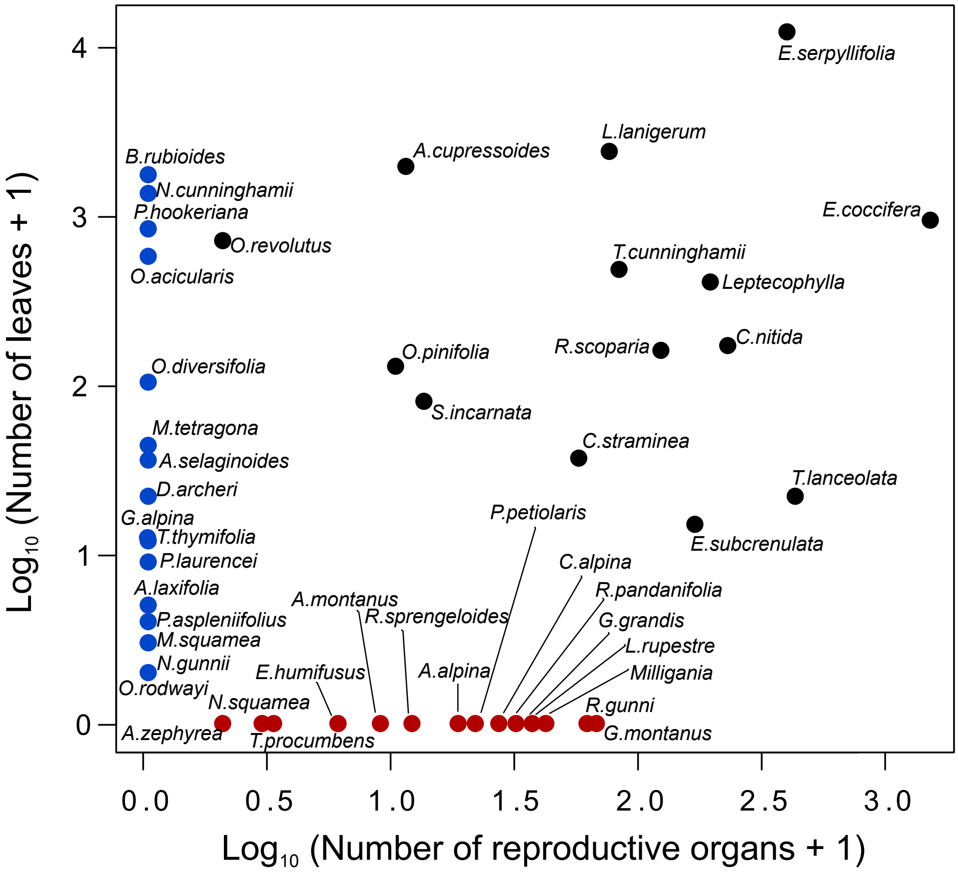

Figure 2-3 Abundances of species represented in the surface sediment samples at Lake Dobson comparing abundance as leaves and reproductive structures. Species present only as reproductive structures (red), species present only as leaves (blue), and species present as both leaves and reproductive structures (grey).

Table 2-1 List of species and number of organs within surface sediments from Lake Dobson, grouped by clade and family.

Group-family	Species	Leaves	Reproductive structures	Presence in catchment
Gymnosperms – conifers				
Cupressaceae	*Athrotaxis cupressoides* D.Don	1955	10	Common throughout in fire refuges
	Athrotaxis selaginoides D.Don	35	-	Absent from catchment
	Athrotaxis laxifolia Hook.	4	-	Very rare, few plants around the lake
	Diselma archeri Hook.f.	21	-	Common in alpine areas
Podocarpaceae	*Phyllocladus aspleniifolius* (Labill.) Hook.f.	3	-	Rare, isolated plants near lake
	Pherosphaera hookeriana W. Archer	836	-	Common throughout in fire refuges
	Microcachrys tetragona (Hook.) Hook.f.	43	-	Common, especially at high altitude
	Podocarpus lawrencei Hook.f.	8	-	Common at mid and high altitude
Angiosperms – dicotyledons and basal angiosperms				
Asteraceae	*Olearia pinifolia* (Hook.f.) Benth.	128	9	Common, except in alpine areas
	Ozothamnus rodwayi Orchard	1	-	Common
Casuarinaceae	*Allocasuarina zephyrea* L.A.S. Johnson	-	1	Absent from catchment
Cunoniaceae	*Bauera rubioides* Andrews	1748	-	Common throughout
Ericaceae	*Acrothamnus montanus* (R.Br.) Quinn	-	6	Common at mid altitudes

	Cyathodes straminea R.Br.	36	54	Common throughout
	Epacris serpyllifolia R.Br.	12205	381	Very common throughout
	Leptecophylla juniperina (J.R.Forst. & G.Forst.) C.M.Weiller	405	186	Common, except in alpine areas
	Planocarpa petiolaris (DC.) C.M.Weiller	-	19	Common at mid to high altitude
	Richea gunnii Hook.f.	-	32	Restricted to boggy areas
	Richea pandanifolia Hook.f.	-	24	Common throughout
	Richea scoparia Hook.f.	159	117	Very common throughout
	Richea sprengelioides (R.Br.) F.Muell.	-	8	Very common throughout
	Sprengelia incarnata Sm.	79	12	Moderately common near lake
	Trochocarpa cunninghamii (DC.) W.M.Curtis	481	79	Common near lake
	Trochocarpa thymifolia (R.Br.) Spreng.	11	-	Very common throughout
Haloragaceae	*Gonocarpus montanus* (Hook.f.) Orchard	-	50	Moderately common
Myrtaceae	*Eucalyptus coccifera* Hook.f.	939	1449	Common, except in alpine areas
	Eucalyptus subcrenulata Maiden & Blakely	14	161	Common near lake
	Leptospermum lanigerum (Aiton) Sm.	2400	72	Common near lake
	*Leptospermum rupest*re Hook.f.	-	31	Common near lake
	Melaleuca squamea Labill.	2	-	Moderately common near lake
Nothofagaceae	*Nothofagus cunninghamii* (Hook.) Oerst.	1352	-	Common up to the tree line

	*Nothofagus gunn*ii (Hook.f.) Oerst.	2	-	Rare
Proteaceae	*Orites revolutus* R.Br.	714	1	Very common throughout
	Orites acicularis (R.Br.) Roem. & Schult.	574	-	Very common throughout
	Orites diversifolius R.Br.	103	-	Common low to mid altitude
Rubiaceae	*Coprosma nitida* Hook.f.	170	219	Very common throughout
Rutaceae	*Nematolepis squamea* (Labill.) Paul G.Wilson	-	2	Absent?
Santalaceae	*Exocarpos humifusus* R.Br.	-	4	Common mid to high altitude
Tremandraceae	*Tetratheca procumbens* Gunn ex Hook.f.	-	2	Rare, isolated plant near the lake
Winteraceae	*Tasmannia lanceolata* (Poir.) A.C.Sm.	21	411	Common, especially at high altitude
Angiosperms – monocotyledons				
Asteliaceae	*Astelia alpina* R.Br.	-	12	Common
	Milligania spp.	-	32	Alpine waterlogged areas
Cyperaceae	*Carpha alpina* R.Br.	-	20	Rare, few plants near lake
	Gahnia grandis (Labill.) S.T.Blake	-	28	Rare, few plants near lake
Pteridophyta (ferns)				
Gleicheniaceae	*Gleichenia alpina* R.Br.	11	-	Common near lake

The 15 most common species accounted for 94% of the total number of reproductive organs. The assemblages of reproductive organs (Fig. 2-4) were dominated by the endemic tree *Eucalyptus coccifera* from Myrtaceae (37%), the shrubs *Epacris serpyllifolia* (15%), *Tasmannia lanceolata* (11%), and *Coprosma nitida* (6%). Reproductive organs also revealed the presence of herbs species (monocotyledonous and dicotyledonous) such as *Gahnia grandis*, *Carpha alpina*, *Astelia alpina*, and *Gonocarpus montanus*, which were undetectable from the leaf assemblages. The reproductive structures also increased the taxonomic resolution for the Ericaceae family (one of the most important families in sub-alpine/alpine Tasmania), expanding the number of identified species from seven to twelve (Table 2-1).

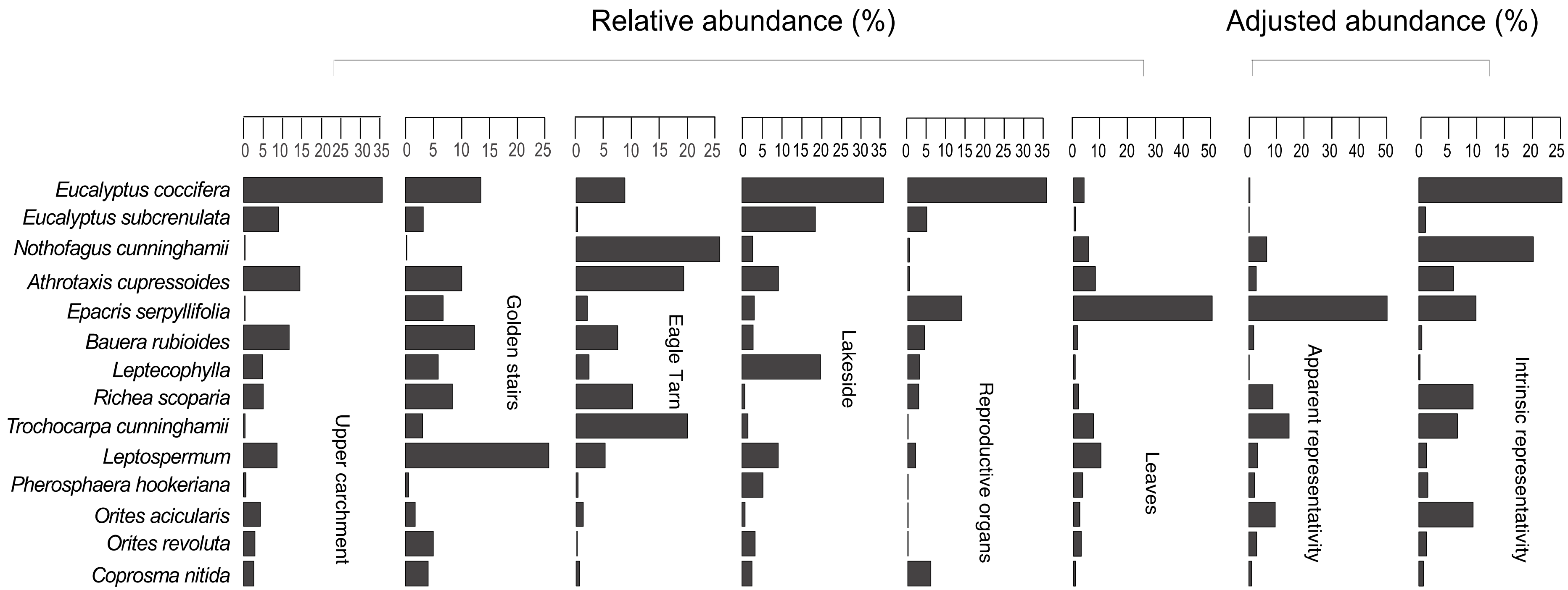

Figure 2-4 Relative abundances of most common species in modern sediments of Lake Dobson, and their representation in the areas of vegetation: Upland vegetation; Golden Stairs Stream; Eagle Tarn Stream vegetation; Lakeside vegetation; Reproductive organs; Leaves. Adjusted abundance expressed as apparent representativity and intrinsic representativity.

2.4.2 Correlations of relative abundance

The reproductive assemblages showed considerably weaker correlations with each of the vegetation types than did the leaf assemblages (Table 2-2). In fact, the lakeside vegetation was the only area of vegetation that showed a positive and significant correlation with the floristic signature of reproductive organs. In contrast, total macrofossil abundance (i.e. leaves and reproductive structures) strongly improved the ability to predict all the areas of vegetation, although the agreement was, once again, particularly strong for the lakeside vegetation and the vegetation along Eagle Tarn Creek (Table 2-2).

There were positive correlations of leaf counts between the leaf assemblages and the relative abundance of the same species in the standing vegetation for three of the investigated areas of vegetation (Table 2-2). The strongest relationship was with the vegetation along Eagle Tarn Creek, although the correlation with the lakeside vegetation was almost as strong. In contrast, the remaining two areas representing the vegetation in the upper catchment and the vegetation along the Golden Stairs Creek showed a negative and a weak positive correlation, respectively (Table 2-2).

2.4.3 Leaf mass per area (LMA)

The representation of plant species in sediments was not related to their values LMA (see Table 6-1 in Appendix 1) with weak and non-significant association between values of LMA and the representation of species in sediments of Lake Dobson (*rho* = 0.047, P = 0.84).

Table 2-2 Spearman rank correlation values (rho) between total plant representation, leaves and reproductive organs in the sediment samples of Lake Dobson, and selected areas of the surrounding vegetation (% abundance). P-values = * < 0.05; ** < 0.01; *** < 0.001.

	Percentage of relative abundance			
	Subfossil leaves	Reproductive structures	Total sum of macrofossils adjusted	# leaves adjusted by area
Relative abundance				
Lakeside vegetation	0.53*	0.44*	0.74***	0.76***
Golden Stairs Creek	0.18	0.3	0.38*	0.25
Eagle Tarn Creek	0.67***	0.31	0.63***	0.54*
Upland vegetation	-0.02	0.25	0.28	0.31
Number of leaves				
Lakeside vegetation	0.69***			
Golden Stairs Creek	0.25			
Eagle Tarn Creek	0.67***			
Upland vegetation	-0.03			

2.4.4 Leaf counts and leaves adjusted by area

Adjusting the number subfossil leaves in an area basis improved the ability to predict the source vegetation for three of the investigated areas compared to leaf counts (Table 2-2). However, correlation values and significance levels are different from those founded using total plant material. Particularly, on this total leaf area representation the vegetation along the Eagle Tarn Creek exhibited a much lower and less significant correlation value with the leaf assemblages.

2.4.5 Differential leaf production

The shrub species produced many more leaves per ground area of vegetation than the tree species (see Table 6-1 in Appendix 1). In particular, the *Eucalyptus* species produced many fewer leaves than *N. cunninghamii* or any other microphyllous shrub species from Ericaceae (*Epacris serpyllifolia, Leptecophylla juniperina, Trochocarpa thymifolia*), Myrtaceae (*Leptospermum lanigerum),* and Cunoniaceae (*Bauera rubioides*). Moreover, the differential productivity of leaves was strongly correlated with the abundance of leaves of the same taxa represented in sediments (Table 2-2).

The correlation between leaf assemblages and litter samples was also low and non-significant (*rho* = 0.44, *P* = 0.097). However, expressing leaf counts in an area basis for litter and subfossil samples, strongly improved the correlation (*rho* = 0.68; *P* = 0.007). Overall, results of this analysis showed not significant differences in mean leaf size among the majority of species in the lake sediments and forest litter. The exception among the eight species evaluated was *L. lanigerum* (Fig. 2-5).

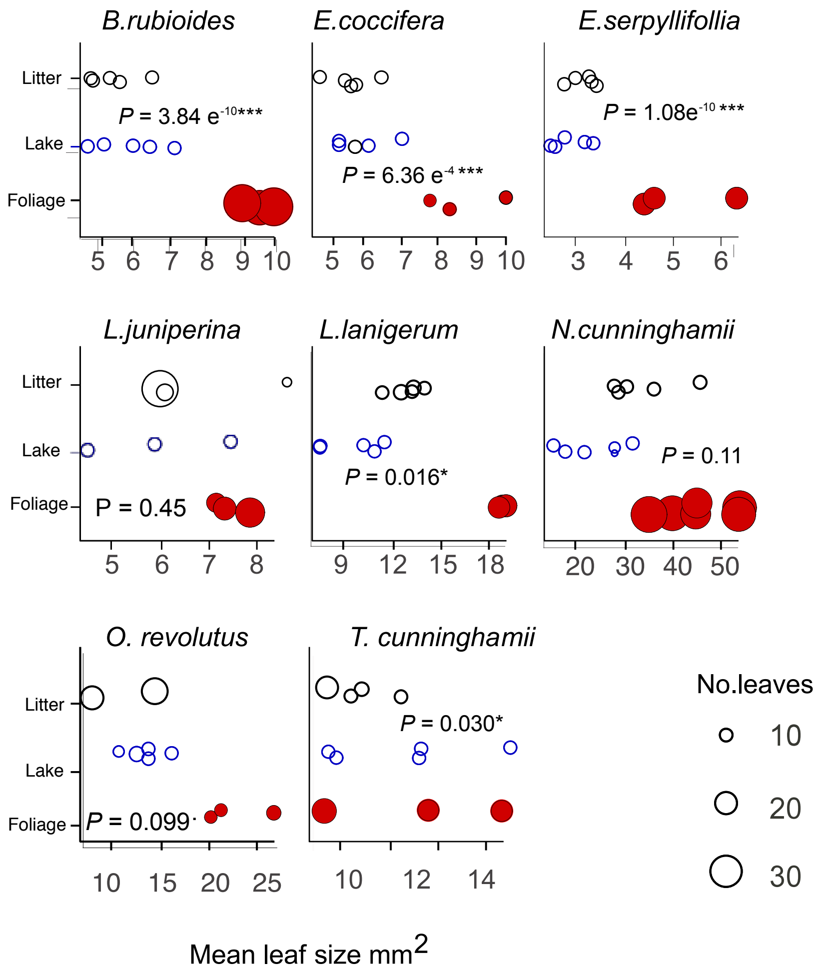

Figure 2-5 Comparison leaf size among foliage, litter and lake sediments.

Significance values from Analysis of Variance: 0 = '***', 0.001 = '**', 0.01 = '*', 0.05 = '.', 0.1 = ' '.

2.5 Discussion

2.5.1 Origin of the macrofossil material

Several lines of evidence suggest that the plant remains recorded in the sediments of Lake Dobson are likely to be almost exclusively derived from vegetation close to the lake (i.e. lakeside and Eagle Tarn Creek vegetation). Allochthonous elements from distant communities such as *Nothofagus gunnii* and alpine conifers are rare and only a few fragments of robust members of the alpine communities, such as the dwarf conifers *Microcachrys tetragona* and *Diselma archeri*, are represented in the modern sediments of the lake. This input of alpine elements from upper parts of the catchment may have occurred via Golden Stairs Creek that links the Mawson Plateau with Lake Dobson (Fig. 2-1). *Nothofagus gunnii* is only deciduous species marginally represented (1 leaf) in the sediments of Lake Dobson, and although this species sheds a high amount of leaves, its rarity in the sediments can be attributed to its near absence in the catchment of the lake. The closest *N. gunnii* to Lake Dobson is a single plant above Eagle Tarn (~180 m away at 42° 68' S, 146°59' E), and the nearest known population is at the Tarn Shelf (~1.5 km away at ~42°68', 146°57' E). Thus, the sparse presence of this species in sediments is likely result of wind or water transportation.

In contrast, common tree and shrub species in closer areas of vegetation are well represented in the sediments, whereas uncommon species in both, standing vegetation and leaf litter (e.g. herbs) were rarely recorded in sediments. This result supports similar findings by Burnham (1993), Greenwood (1992), and Steart *et al*. (2005) indicating that rare species in the standing vegetation will be rare or absent from the forest litter, and therefore, equally rare in depositional settings.

Overall, the plant remains recorded in the sediments of Lake Dobson are well preserved, and present little fragmentation. The vast majority of the leaf types belong to sclerophyllous species, which are potentially robust enough to be transported and preserved, compared to more fragile leaf types. However, it is also known that leaves have only a limited transport and reworking potential compared to other plant structures such as pollen (Spicer 1991). Furthermore, the potential transport by water of plant remains from alpine communities above Lake Dobson (i.e. Mt. Mawson Plateau; Fig. 2-1) is restricted to the Golden Stairs Creek that flows partly underground into the lake.

Several studies have recognised the distance of the plant community to the site of deposition as being critical in the final representation of plant species in sediments (Ferguson 1985; Ferguson 2005; Gastaldo and Demko 2010; Rowell et al. 2001; Spicer 1989; Spicer and Wolfe 1987). Thus, species living close to the site of deposition have more chances to be represented in the sediments than plants living in distant communities (Birks 2001; 2007; Birks and Birks 1980; Gastaldo et al. 1996; McQueen 1969; Rich 1989; Rowell et al. 2001; Spicer and Wolfe 1987). The results presented in this study corroborate the same pattern, and support that the distance of the plant community is an effective filter in determining the final representation of plant parts in the sediments of Lake Dobson. Although there are differences in significance and order of importance in which the areas of vegetation are predicted (Table 2-2), two of the closer areas of vegetation to the lake (the lakeside vegetation and the area of vegetation along Eagle Tarn Creek) are predicted to be the primary sources of plant material incorporated in the sediments Lake Dobson.

Additional supporting evidence for the local origin of the plant material is the presence of different plant organs representing the same species. This feature is considered to indicate parautochthony or autochthony, mainly because different plant parts may have differing transport potential (Ferguson 1985; Ferguson 2005; Gastaldo and Ferguson 1998; Gastaldo et al. 1996; Spicer 1989). Thus, it is likely that the mixture of plant parts (i.e. leaves, seeds, fruits and delicate floral structures) recorded in the modern sediment samples of Lake Dobson has undergone limited transport from their source vegetation, and is probably local in origin.

Similarities in leaf size among litter and sediment samples also suggest, despite the small sample size that leaves in the lake sediments are probably derived from plants living in close proximity to the lake. Overall, the non-significant differences in mean leaf size (Fig. 2-5) between the two groups suggest reduced transport and sorting of plant parts. The only exception seems to be the shrub *Leptospermum lanigerum* (Fig. 2-5). It is possible that differences in leaf sizes for this species are due to moderate transport from areas above the lake, especially the Golden Stairs, where its abundance is much higher than other vegetation areas. However, if transportation of plant material occurred from more distant plant communities, we could expect a reduction in leaf size among the taxa entombed in sediments (Greenwood 1992). Thus, taphonomic biases based on selection of leaf sizes due to transportation for systems similar to Lake Dobson are likely to be small.

2.5.2 Other predictors of fossil deposition

The number of subfossil leaves for each species represented in sediment does not accurately predict species abundances in the standing vegetation, even in terms of rank-order (Fig. 2-4). However, this discrepancy is partially resolved when numbers of subfossil leaves are adjusted to allow for differences in leaf size (Table 2-1). On this per leaf area basis, the agreement between the representativity of dominant species is particularly strong for the lakeside vegetation. The ability of this correction to improve the agreement between the abundance of species in sediments and the abundance of the same species in the source vegetation, can easily be seen by considering the differences in leaf size between the two dominant species in sediments and standing vegetation, respectively. *Epacris serpyllifolia* (mean leaf area of 4.2 mm^2) dominated the subfossil assemblages, whereas *Eucalyptus coccifera* (mean leaf area of 900 mm^2) is by far the dominant species in the catchment, and lakeside vegetation. An interpretation of the vegetation around Lake Dobson based solely on leaf counts from sediments could lead to erroneously conclude that *E. serpyllifolia* is the dominant species around the lake. These findings are consistent with those of early studies, showing that the number of leaves in litter samples does not predict accurately the ranking of species in the standing vegetation particularly when there are big differences in leaf size (Burnham et al. 1993; Collison 1983; Drake and Burrows 1980; Hill and Gibson 1986; Spicer and Wolfe 1987; Steart et al. 2005).

The relationship between subfossil leaves and closer areas of vegetation around Lake Dobson significantly improved when using the number of leaves per ground area of vegetation produced for each species (Table 2-1). Although this adjusted representativity is only an approximation of the likelihood for each one of the most common species to be represented in the sediments, it shows clearly the differing number of leaves that each species can potentially shed, and relative importance when scaled to their abundance in the standing vegetation.

The best examples to explain these considerations are again *Epacris serpyllifolia* and *Eucalyptus coccifera*. The former is a minor component of the vegetation with the higher production of leaves per unit area, whereas the latter is the dominant tree species in the lakeside vegetation (Fig. 2-4 and Table 6-1 in Appendix 1). It is credible that the strong under-representation of *E. coccifera* in the sediments compared to their dominance in the standing vegetation is largely caused by a combination of taphonomic factors. In particular, the low number of leaves produced per unit ground area (Table 6-1 in Appendix 1), the poor aerial dispersion of the leaves limiting their incorporation in sediments, and the restricted preservation potential of the leaves due to their inability to float (Carpenter and Horwitz 1988; Hill and Gibson 1986; Steart et al. 2005). This result suggests that number of leaves entombed in sediments must be used with caution when interpreting fossil records.

The case of *Nothofagus cunninghamii* is slightly different. This species appears to be over-represented in sediments once we allow for total leaf area particularly compared to the relative abundance of this species in the lakeside vegetation. *Nothofagus cunninghamii* has a much lower abundance in the lakeside vegetation compared to the *Eucalyptus* species, although is the fifth more common species represented in leaf assemblages (Fig. 2-4). This species also presents a moderately low production of leaves per ground area of vegetation compared to the majority of shrub species, but higher leaf production compared to the *Eucalyptus* species (see Table 6-1 in Appendix 1). These results are in agreement with the differential leaf-litter production relatively to standing biomass observed by Steart *et al*. (2005) for *Nothofagus cunninghamii* and *Eucalyptus regnans* in two different forest systems in Australia. The differences in production of leaves between these two species could also explain why Carpenter and Horwitz (1988) founded that *Eucalyptus obliqua* was rarely recorded among litter samples in two creeks in Tasmania. However, the over-representation of *Nothofagus cunninghamii* observed by the last authors was not associated, in the case of Lake Dobson, to dominance of the species in areas of vegetation close to the lake. Furthermore, the presence of *Eucalyptus coccifera* is consistently higher in three out of four areas of vegetation (Fig. 2-4), although the abundance of *Nothofagus cunninghamii* was higher along Eagle Tarn Creek. It appears, that different taphonomic factors than those related to abundance in the source vegetation, proximity to the site of deposition and rates of leaf production are playing a major role in the final representation of *Nothofagus cunninghamii* in sediments.

Additionally, the representation of plant species in sediments was not predicted by their individual values of leaf mass per area (LMA). This result is unexpected since it is generally accepted that plants producing robust leaves (e.g. high LMA) will be strongly represented in sediments (Steart et al. 2005). However, some studies have suggested that high values of LMA also correlate well with high values of leaf life span of species (Anten 2002; Reich et al. 1998; Wright and Cannon 2001). Thus, species with high LMA may potentially retain foliar organs for longer times, and therefore shed fewer leaves per unit time than plant species with lower leaf investments, although this needs to be corroborated with empirical data.

2.5.3 *Representativity of plant macrofossils*

The apparent representativity index for each of the common species provide insights into the relationship of abundance of leaves deposited from a specific taxon present in the sediments, and the frequency of the same taxon in the source vegetation. However, resulting estimates of the representation of individual species are only relative to other species in the assemblage. Thus the representativity of a given species may vary markedly depending on the system in which is measured providing a distorted reconstruction of the species dominance in the standing vegetation (Fig. 2-4). The apparent representativity index indicates the bias against the preservation of species due to the cost of transport, decay and differential production in number of leaves.

Accounting for the differential production of leaves that each species may produce, allows for an estimation of the number of leaves that can be potentially incorporated in sediments. Particularly, the incorporation of specific intrinsic factors in the calculation of representativity (equations a and b) provided a more realistic quantification of the contribution and representation of different tree and shrub species present in the sediments of Lake Dobson (Fig. 2-4).

The intrinsic representativity index developed in this study indicates the bias against preservation of a species due to the cost of transport and decay, and provides a more accurate picture of the relationship of abundance between leaves assemblages in sediments and their source vegetation (Fig. 2-4).

2.6 Conclusions

Processes of fossilisation of plant remains in Southern Hemisphere may differ from typical taphonomic processes previously studied in the Northern Hemisphere. Particularly, austral temperate floras differ in having a much higher proportions of evergreen species compared to the major deciduous component of the vegetation in temperate northern latitudes (Box 2002; Jordan 2011; McGlone et al. 2004). These differences may have taphonomic implications because thick coriaceous evergreen leaves have different taphonomic properties (i.e. potential for transportation, buoyancy and preservation) than thin papery leaves of deciduous species (Ferguson 1985; Spicer 1981; Steart et al. 2002). In particular, temperate floras from Australia exhibit a high diversity of microphyllous and sclerophyllous evergreen species, and therefore, plant species producing these leaf traits can be strongly represented in fossil deposits. The data from modern sediments of Lake Dobson corroborate some of the taphonomic patterns observed in northern latitudes studies, although differences between systems and geographic locations also exist. Particularly, leaves numerically dominated the plant assemblages from Lake Dobson over reproductive structures (Fig. 2-2). This pattern is consistent with the dominance of leaves and the uncommon presence of reproductive structures founded in Quaternary and Tertiary fossil floras from Australia (Christophel 1984; Christophel and Basinger 1982; Hill 1983; Jordan 1997; Jordan et al. 1991; Jordan et al. 1995). However, it contrasts markedly to Northern Hemisphere fossil deposits where reproductive structures are generally more common than leaves (Birks and Birks 1980). Despite the dominance of foliar organs in sediment of Lake Dobson, the analysis of reproductive structures increases the taxonomic resolution, and provides insight into the relationship between accumulation of plant parts and the original composition of species in the source vegetation.

Particularly, reproductive organs may provide information regarding the presence of herbaceous plant species, from which leaves are generally not abscised from the parent plant, and are therefore absent from leaf assemblages.

The data from modern sediments of Lake Dobson also support that distance of the plant community to the depositional site as one of the critical factor affecting the final representation of species in sediments. This finding is consistent with studies in Northern Hemisphere systems (Ferguson 1985; Ferguson 2005; Gastaldo and Demko 2010; Spicer 1989; Spicer and Wolfe 1987). Furthermore, floristic composition of the plant assemblages strongly agrees with the composition of species in closer areas of vegetation. However, the number of leaves in sediments does not predict the same abundance of the species in the standing vegetation, mainly because the large differences in leaf size and rate of production that exist among tree and shrub species. This observation is consistent with early studies in Australian *Nothofagus* and *Eucalyptus* dominated forests (Steart et al. 2005).

Paleoreconstructions of the original forest richness based solely in the number of fossil leaves present in the sediments could lead to a bias towards the over-representation of species producing small leaves, and high amount of foliar organs. Particularly, because shrub species with small leaves produce much higher number of leaves per unit area than tree species with bigger leaves. Consequently, the chances that species have of being represented in sediments are potentially higher if other taphonomic factors are not affecting their deposition and preservation in sediments. The benefits of including modern information of the deposition of plant organs in past plant reconstructions studies may have important implication for the interpretation of fossil records.

3 Chapter 3 – Plant macrofossil evidence for local glacial survival, and postglacial migration in south-central Tasmania

3.1 Abstract

Treeline investigations spanning the Lateglacial-Holocene transition have important implications for understanding how fast plant species have responded to past climatic and environmental changes, and how species may respond to future climate variations. Almost all Last Glacial pollen records from Tasmania, southernmost Australia, are interpreted as showing widespread treeless conditions during the Last Glacial Maximum (LGM), although there is also increasing molecular evidence supporting the glacial survival of tree species in unexpected areas of refugia. In such situations where pollen and molecular evidence are contrary, plant macrofossils can provide information to clarify the role of local glacial survival versus the postglacial colonisation of plant species in the assembly of treelines at the Last Glacial-Interglacial Transition (~ 18 300–11 600 cal yr BP).

The plant macrofossil evidence from a subalpine lake deposit in southern Tasmania strongly suggests that some alpine conifer species may have survived the last glaciation locally, as they were part of the local vegetation shortly after deglaciation was completed (probably before 14.6–15.1 cal kyr BP). The subsequent expansion of the temperate tree *Nothofagus cunninghamii* synchronous with rising temperature at the Last Glacial-Interglacial transition argues that that species also survived locally. In contrast, postglacial dispersal may explain the delayed arrival of *Eucalyptus coccifera* and *E. subcrenulata* suggesting that the modern configuration of the

vegetation – i.e. *Eucalyptus* open woodlands – was not reached before ~8 cal kyr BP, even though climatic and fire conditions for the establishment of these species became suitable earlier. This study of past vegetation changes, around a currently near-treeline lake provides evidence of the variability in plant responses and assembly of subalpine/alpine plant communities as a response to the environmental variations for a period of time which is not yet well understood in areas of the Southern Hemisphere: The transition from Lateglacial to interglacial conditions.

3.2 Introduction

One of the great controversies in modern ecology has focussed on how forest species survived the ice age climates of the Last Glacial Maximum (LGM; ~24 – 18 thousand years ago) and then recovered to achieve their current ranges. The traditional glacial refugial model holds that species survived in areas with climates similar to those in which these species now occur, and underwent rapid post-glacial migration. Typically, the inferred refugia were significantly downslope or closer to the equator than at least some current populations of the species. This view was supported by fossil evidence from the northern hemisphere (e.g. Davis et al. 1986). However, this model implies seemingly impossible rates of dispersal for some species (Clark et al. 1998; Ritchie and MacDonald 1986). The alternative view (the microrefugial model) holds that many species occurred in numerous small pockets of habitat across the current range of the species. This view is supported by molecular (DNA) evidence (e.g. Magri et al. 2006; McLachlan et al. 2005). The complication with this model is that it implies that many species survived in conditions well outside their current environmental ranges, implying changes in existing realised niches (Worth et al. 2014).

One important way of testing these alternative views is to use fossil evidence to investigate how species in areas of steep ecological gradients have reacted to past environmental change. Alpine treelines are particularly useful for such investigations (Dullinger et al. 2004; Körner 1998; Körner and Paulsen 2004; Kupfer and Cairns 1996). Many plant species living near treelines will be particularly responsive to climate change as they are close to the physiological limits of their distribution (Körner and Paulsen 2004; Lotter and Birks 2003; Tinner 2007). Although natural and anthropogenic disturbances can contribute (Richardson and Friedland 2009; Slatyer and Noble 1992; Tinner 2007), the altitudes of treelines appear to be most strongly influenced by temperature, particularly the warmth of the growing season (Daubenmire 1954; Heiri et al. 2006; Holtmeier and Broll 2007; Körner 1998; Körner and Paulsen 2004; Lotter and Birks 2003; Richardson and Friedland 2009; Slatyer and Noble 1992).

The Last Glacial-Interglacial Transition at the treeline has been widely studied in the Northern Hemisphere (Barnekow 1999; Birks and Bjune 2010; Tinner and Kaltenrieder 2005, and references therein). However, much remains to be understood about the changes of the vegetation at the treeline during the transition in the Southern Hemisphere (Hopf et al. 2000; Martin 1986; Martin 1999a; McGlone et al. 2010; McKenzie 1997). South-eastern Australia, and particularly Tasmania, has been the subject of intense fossil pollen investigation during the past 35 years (Colhoun 1992; Colhoun 1996; Colhoun et al. 1999; Colhoun and Shimeld 2012; Colhoun et al. 1991; Dodson 1998; Dodson 2001; Fletcher and Thomas 2007; Fletcher and Thomas 2010; Macphail 1979; Markgraf et al. 1986). Although these studies have provided important information regarding the late Quaternary vegetation and climatic history of the region, a number of important paleoecological questions remain unresolved. For instance, most Last Glacial Maximum (LGM: 24 000–18 000 years ago; Colhoun and Shimeld 2012) pollen studies in western Tasmania indicate the ubiquitous presence of alpine grassland and herbfields at low to mid-altitude sites (Colhoun 2000; Colhoun et al. 1999; Colhoun and Shimeld 2012; Colhoun and Van De Geer 1986b). These pollen assemblages have been interpreted as indicating a treeline depression ranging from 500 to 800 m, and consequently, a temperature drop of 3–6°C during the LGM. However, resolving the local presence of trees and shrubs by means of pollen analysis in treeless situations (e.g. alpine late-glacial landscapes), or determining the past position and composition of the treeline and glacial refugia is challenging (Barnekow 1999; Birks 1994; Birks 2001; Birks 2003; Birks and Birks 2000; Krebs et al. 2004; Ritchie 1995; Tinner and Theurillat 2003). In particular, wind dispersed pollen types blown-upslope may confound the signal of local low-pollen-producing vegetation at high elevation sites (Birks 1994; Birks and Birks 2000; Birks and Bjune 2010; Brewer et al. 2002; Eide et al. 2006).

Molecular vegetation studies strongly support the idea that many important plant taxa (*Nothofagus cunninghamii*, *Eucalyptus* subgenus *Symphyomyrtus*, *Eucalyptus* subgenus *Eucalyptus* and *Tasmannia lanceolata*) survived the LGM in multiple glacial refugia across Tasmania (McKinnon et al. 2004; McKinnon et al. 2001; Nevill et al. 2008; Nevill et al. 2010; Worth et al. 2010; Worth et al. 2009). Additionally, the molecular evidence suggests that these tree species have shown very low mobility and often survived in areas that would be unexpected based on their modern bioclimatic ranges and our current understanding of last glacial environments (Worth et al. 2014; Worth et al. 2009). The molecular studies suggest that pollen reconstructions may have underestimated the presence of woody vegetation in the landscape during the LGM, and therefore, the treeline model of community assembly during the Last Glacial-interglacial transition needs to be reconsidered.

The area of Lake Dobson in Mount Field National Park, south-central Tasmania provides an ideal location to investigate the role of local glacial survival versus the postglacial colonisation of plant species in the assembly of treelines at the Last Glacial-interglacial transition. In particular, Lake Dobson is strategically located just ~ 190 m vertically below the modern treeline, and therefore, close to the 10°C isotherm of the warmest month that predicts the limit of the tree growth (Kirkpatrick 1982; Kirkpatrick 1997; Kirkpatrick and Fowler 1998; Pauley 2004). It has a sediment core extending to the Lateglacial (~15 cal kyr BP), including a charcoal record (Rees et al. 2015) that provides the opportunity to assess whether changes in vegetation through time are mainly driven by climate and/or other environmental factors such as fire. Additionally, the history of the vegetation in the area has been previously studied from a pollen sequence of similar age at Eagle Tarn (Colhoun 1996; Macphail 1979; Markgraf et al. 1986).

In this study, plant macrofossil stratigraphic evidence from the sediments of Lake Dobson is presented to gain insight into the models of plant community assembly at the treeline during the Last Glacial-Interglacial Transition. This study particularly exploits the capacity of macrofossils to provide direct evidence of the presence of a specific taxon in the local paleovegetation that results from the high taxonomic resolution and limited dispersal of macrofossils (Birks 2001; Birks 2007; Birks and Birks 1980; Dieffenbacher-Krall 2007; Huntley 1996; Jackson and Booth 2007). The study specifically aims to answer the following questions. 1) Is there evidence to support the idea that treeline and alpine plant communities assembled from local glacial survivors? 2) Is there any time lag in the arrival of tree taxa to sub-alpine areas of Mt. Field after the glacial retreat? 3) How well does the plant macrofossil record track regional climate reconstructions and the evidence from pollen studies?

3.3 Material and methods

3.3.1 Site location

Lake Dobson (42°41.0' S, 146°35.4' E; 1034 m a.s.l.) is located in the subalpine vegetation zone in Mount Field National Park, south-central Tasmania (Fig. 3-1). The lake covers *c*. 5.7 ha in the base of a small cirque that was occupied by a glacier during the last glaciation (Barrows et al. 2002; Macphail 1979). The hydraulic catchment of the lake is ~1 km^2 (Jordan et al. 2007). A basal organic age presented by Rees et al. (2015; see Table 7-1 in Appendix 2); when calibrated suggests that glacial retreat at Lake Dobson may have occurred at some time before 14.6–15.1 cal kyr BP. This date is in reasonable agreement with the age range 14.1–16.6 cal kyr (12 960 ± 950 ^{14}C yr BP) proposed for Eagle Tarn (Fig. 3-1), centred ~ 400 m north of Lake Dobson (Barrows et al. 2002).

Most of Tasmania has a temperate climate with mild summers or cool summer in higher plateau areas (Stern et al., 2000). However, the park is situated in a transitional area between a perhumid region of wet vegetation types, including extensive wet sedgeland/heaths and cool temperate closed forests extending to the west, and a subhumid region of *Eucalyptus* open forests and grasslands extending to the east (Harris and Kitchener 2005; Macphail 1979; Read 1999). Climatic parameters generated by ANUCLIM (Houlder et al. 2003) indicate that annual mean temperature in the Lake Dobson area is 6.2°C and annual mean precipitation is 1454 mm. The climate is equable, with mean temperatures of warmest and coldest quarter being 10.3°C and 2.3°C, respectively.

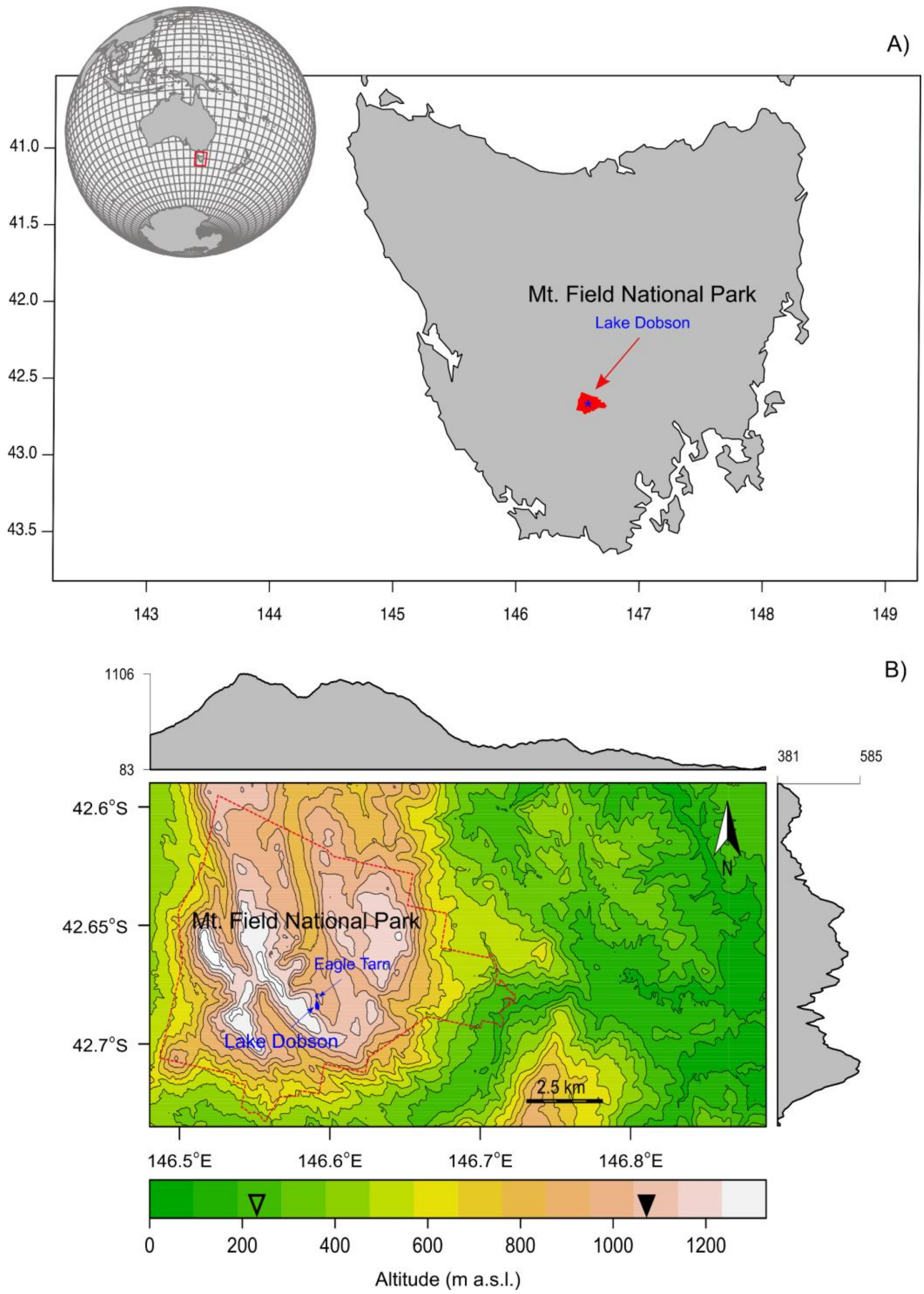

Figure 3-1 Site location (a) Mount Field National Park south-central Tasmania. (b) Topographic map showing altitude profile (m a.s.l.) in the area around Lake Dobson (dashed red line indicates the limit of the park). The closed triangle indicates the current altitude of the treeline, and the open triangle the treeline altitude with a temperature drop of ~6°C at the LGM.

3.3.2 Present day vegetation

The catchment of Lake Dobson contains several vegetation types (Macphail 1979; Ogden and Powell 1979). Above the altitudinal treeline (~ 1220 m a.s.l. and approximately 190 m above the lake) the vegetation is characterised by a mosaic of sedgeland, herbfield, cushion plants, sclerophyll heaths and patches of dwarf coniferous species including *Diselma archeri*, *Pherosphaera hookeriana*, *Microcachrys tetragona* and *Podocarpus lawrencei* (Crowden 1999; Harris and Kitchener 2005; Kirkpatrick 1982). Woodlands, heaths, and sedgelands occupy areas below the treeline. Woodlands dominated by *Eucalyptus* species (*E. coccifera* and *E. subcrenulata*) are interspersed by stands of montane rainforest dominated by *Nothofagus cunninghamii* and *Athrotaxis cupressoides*. Heaths are mainly dominated by shrub species from Ericaceae, Myrtaceae, Proteaceae and Asteraceae, while sedgeland vegetation is dominated by members of Cyperaceae, Restionaceae, Asteliaceae and Gleicheniaceae (Crowden 1999; Harris and Kitchener 2005; Macphail 1979; Ogden and Powell 1979).

3.3.3 Past vegetation studies

Pollen investigations in subalpine areas of Mount Field National Park and elsewhere in mountain sites from southern Tasmania show similar patterns of vegetation change during the Lateglacial and Holocene (Colhoun 1996; Colhoun and Shimeld 2012; Macphail 1979). In particularly, pollen records from the Lake Dobson area have suggested that during the Lateglacial before ~13.4 kcal yr BP (11 500 ^{14}C yr BP), the vegetation was essentially treeless and dominated by non-arboreal pollen types or fellfield associations (i.e. Poaceae and Asteraceae). After this period, pollen assemblages show a sequence of vegetation types in which conifers and sclerophyllous heath vegetation alongside with *Eucalyptus* appear around 11 500–10 000 ^{14}C yr BP. Following, the transient establishment of *Eucalyptus*/*Phyllocladus* associations at *c*. 9 500 ^{14}C yr BP; cool temperate rainforest dominated by *Nothofagus cunninghamii* became dominant at c. 10 000 –6 000 ^{14}C kyr BP (Colhoun 1996; Macphail 1979; Markgraf et al. 1986). Finally, pollen records show a reversion (c. 6 000 ^{14}C yr BP) to open canopy woodlands dominated by *Eucalyptus* similar to the modern vegetation in subalpine areas of Mt. Field (Macphail 1975; Macphail 1979).

3.3.4 Core collection, age calibration and age-depth model

The material for the analysis of plant macrofossil was obtained from a ten-meter long, 10 cm diameter sediment core collected from the deepest part of Lake Dobson with a modified Livingston piston corer (Wright et al., 1984) during January of 2010 by Andrew Rees (Victoria University of Wellington), and Les Cwynar (University of New Brunswick). Rees et al. (2015) developed an age model for the Lake Dobson core, based on ten AMS ^{14}C dates (UCI Keck Carbon Cycle AMS Program, University of California, Irvine) of plant macrofossil material. Thus, for the calibration of the radiocarbon dates and building of the age-depth model I followed the methodology proposed by Rees et al. (2015; see Table 7-1; Fig. 7-1 in Appendix 2) using CLAM 2.2 for classical non-Bayesian age modelling (Blaauw 2010), and the Southern Hemisphere curve SHCal13 (Hogg et al. 2013). The age-depth model was constructed using a smooth spline run through randomly sampled point estimates from calibrated dates and iterating this process a thousand times. The smooth spline was weighted by the probabilities of the sampled calibrated years (Blaauw 2010). Calibrated dates are provided in thousands of calibrated years before AD 1950 (cal kyr BP).

3.3.5 Plant macrofossils analysis

The 10 m sediment core was sliced in half lengthwise. One half was divided into 100 10-cm thick sediment samples, which were analysed for plant macrofossils. Each sample therefore represented approximately 100 years (maximum of 250 years and minimum of 30 years). Plant material was extracted from each sediment sample using the general approach of Birks (2007), as follows. Each sample was soaked in a 10% aqueous solution of tetrasodium pyrophosphate until the sediments disaggregated (approximately 14–21 days). Then, sediments were washed gently with tap water through two or three stacked sieves (mesh size of 250 μm, 500 μm, and 1 mm) to concentrate macrofossils. The residues were stored in distilled water and refrigerated prior to sorting under a stereomicroscope at 10-40x magnifications.

Vascular plant remains (i.e. complete and fragmentary leaves, flowers and fruits) were identified to the species level wherever possible by comparison with reference collections held at the School of Plant Science, University of Tasmania, and taxonomic plant descriptions by Curtis (1963; Curtis 1967); Curtis and Morris (1975; 1979; Curtis and Morris 1994); Stevens et al (2004); Weiller (1999); Carpenter et al (2011); and Jordan (1992). The identification of *Eucalyptus* and *Leptospermum* remains was not differentiated to the species level.

To assist with the identification of non-vascular plant remains, reference collection of 62 bryophyte species from the Lake Dobson area, and an additional of 38 species from the Hartz Mountains subalpine area. Leaves from each of these bryophyte species were mounted on microscope slides in phenol glycerine jelly. The taxonomic identification followed George and McCarthy (2006); Malcolm and Malcolm (2006); Seppelt (2004).

3.4 Numerical analyses

3.4.1 Data preparation, plant macrofossil diagram and zonation

Twelve sediment samples lacking plant macrofossil remains were omitted from the analyses, and contiguous samples containing low frequency of plant remains (< 20 remains per sample) were combined, leaving a total of 80 samples. Plant macrofossils counts were transformed to percentage data using the function *percenta* of the PaleoMAS package in R (Correa-Metrio et al. 2011). Plant taxa with less than five occurrences, or that failed to record 5% of representation in the whole set of remaining samples, were grouped into higher taxonomical categories whenever possible; otherwise were excluded. Percentage values were recalculated after exclusion, and the remaining macrofossil sum (47 plant species, and 80 samples) was used to produce plant macrofossil diagrams using the package '*analogue*' in R (Simpson 2007). The plant macrofossil percentages were log-transformed before ordination analysis in order to reduce the asymmetry of the distributions (Legendre and Birks 2012).

For the zonation of the plant macrofossil at Lake Dobson, I applied constrained incremental sums of squares cluster analysis (CONISS; Grimm 1987) after squared root transformation of the percentage data using *vegdist* of the *vegan* package in R (Oksanen et al. 2013), and *chclust* of the *rioja* R-package (Juggins 2009). The number of significant zones in the cluster analysis was assessed through the broken-stick model (Bennett 1996), available in the *rioja* package in R (Juggins 2009).

3.4.2 Gradient analysis

Detrended correspondence analysis (DCA) based on the log-transformed plant macrofossil data with detrending by segments and downweighting of rare taxa (Hill and Gauch 1980; Legendre and Birks 2012) was used to summarise the major underlying pattern and gradient length of the floristic data. This analysis was implemented using the *decorana* function of the *vegan* package in R (Oksanen et al. 2013).

3.4.3 Environmental variables

To investigate the relationship between plant responses and environmental factors over the past 15 thousand years this study used temperature and carbon dioxide data from two Antarctic cores using the EDC3 chronology (Parrenin et al. 2007). The EPICA Dome C ice core (Jouzel et al. 2007a; Jouzel et al. 2007b; Lüthi et al. 2008; Monnin et al. 2001), and the Vostok ice core (Petit et al. 2001; Petit et al. 1999). As complementary paleoclimatic data for temperature and precipitation $\delta^{18}O$ and $\delta^{13}C$ isotopes from speleothems in New Zealand were used (Williams et al. 2004; Williams et al. 2005). Additionally, influx of charcoal particles to the sediments of Lake Dobson (Rees et al. 2015) was derived from the same core as the plant macrofossil.

Because ice core and speleothem records are at higher temporal resolution than the Lake Dobson core, the climate records were binned into comparable time periods to the plant macrofossils data by averaging before ordination analyses. All of the environmental variables were standardised to mean zero and unit variance using the *decostand* function of the *vegan* package in R, method ‘standardize’ (Legendre and Birks 2012). Then, principal component analysis (PCA) was performed on the temperature data (EPICA Dome C, Vostok and $\delta^{18}O$ from NZ) to summarise the main pattern of temperature variation. PCA was used, as this methodology finds the best fit of linear combinations of variables, providing new composite components that are uncorrelated (Birks 2012). The number of statistically significant axes for retention was evaluated by comparison to the broken-stick model.

3.4.4 Canonical correspondence analysis (CCA)

Canonical correspondence analysis (CCA; Ter Braak 1986), implemented in *vegan* (Oksanen et al. 2013) was used to investigate how the changes in vegetation can be explained by a set of environmental predictors, i.e. by changes in temperature, carbon dioxide, precipitation and fire activity. This methodology was selected, as it is the best, for testing hypotheses of biological responses in fossil assemblages due to particular paleoenvironmental variables (Legendre and Birks 2012). The statistical selection of the environmental variables followed the methodology proposed by Borcard et al. (2011) using permutation tests, forward stepwise selection, and parsimonious CCA.

3.5 Results

Numerically, the macrofossil assemblages were dominated by bryophytes accounting for 70% of all macrofossil specimens. A total of 57 species of mosses within 31 families and two liverwort species from two families were recognised (see Fig. 3-3; Fig. 3-4 and Table 7-2 in Appendix 2). The main vascular plant structures recorded in the sediments of Lake Dobson were leaves of tree and shrub species from 29 species in 11 families (see Fig. 3-5; 3-6 and Table 7-2 in Appendix 2). Reproductive structures in both vascular and non-vascular plants were rare. Graminoids and ferns were only represented by a few remains of a few species, such as *Gahnia grandis* from the Cyperaceae, and the ferns *Gleichenia alpina* and *Blechnum* sp. No grasses were observed.

3.5.1 Composition and zonation

A total of 8,545 plant remains were recovered from the sediment of Lake Dobson. The number of remains per sample ranged from 21 to 522 with a mean concentration of 107 fragments per 10 cm of sediment. Five-plant macrofossil zones (LD1-LD5) were distinguished by means of cluster analysis CONISS (Fig. 3-2).

From the beginning of the sedimentary sequence at 1040 cm depth (15.4 cal kyr BP) to the start of Zone LD1 (940 cm depth; 14.9 cal kyr BP), the sediments were almost completely devoid of plant remains. However, a few remains of two bryophyte species with current ecological associations to recently disturbed or burnt habitats i.e. the moss *Polytrichum juniperinum* and the leafy liverwort *Cephaloziella exiliflora*, were recorded at around 15.1 cal kyr BP (970–980 cm).

Zone LD1 (940–715 cm; 14.9–11.8 cal kyr BP) is dominated by high subalpine/alpine plant species (see Fig. 3-3 and Table 7-2 in Appendix 2). In particular, this zone presented high percentages (20–96%) of alpine conifers such as *Diselma archeri*, *Microcachrys tetragona* throughout the zone, and to a lesser extent of *Athrotaxis cupressoides*. *Epacris serpyllifolia* and other alpine/subalpine shrubs such as *Orites acicularis*, *Coprosma nitida* and *Sprengelia incarnata* are also present through this zone reaching an average value of 27%. Few remains (>1%) of the arboreal species *Nothofagus cunninghamii* are recorded at 14.8 and 13.1 cal kyr BP. Additionally, bryophyte assemblages indicate the presence of species that are common today in alpine and subalpine grasslands, heaths and herbfields, and exposed rocky environments i.e. species of *Andreaea*, *Grimmia* and *Bryum* (Table 5-2, Fig. 3-4).

After a gap of *c*. 900 yr from 11.8 to 10.9 cal kyr BP, a major plant transition is recorded in the early Holocene of zone LD2 (680–515 cm; 10.9–6.3 cal kyr BP). A sharp drop in the representation of alpine conifers, from an average representation of 72% in zone LD1, to 27% is recorded. The rainforest tree *Nothofagus cunninghamii* increases its representation in this zone to an average of 23% with a maximum representation peaking around 9.5, 8.8, and 6.8 cal kyr BP. Trace amounts of other rainforest species such as *Phyllocladus aspleniifolius* (9.3 cal kyr BP), are also recorded during this period. Towards the top of the boundary *Eucalyptus* and *Leptospermum,* begin to make an appearance in the record, albeit in small percentages.

Additionally, the bryophyte flora indicates the presence of species that are today characteristic of cool temperate rainforest, and moist/shaded environments, such as the leafy liverwort *Leptoscyphus* (9.8–7.4 cal kyr BP) and the mosses *Camptochaete arbuscula* and *Weymouthia spp*. (Table 5-2, Fig. 3-2).

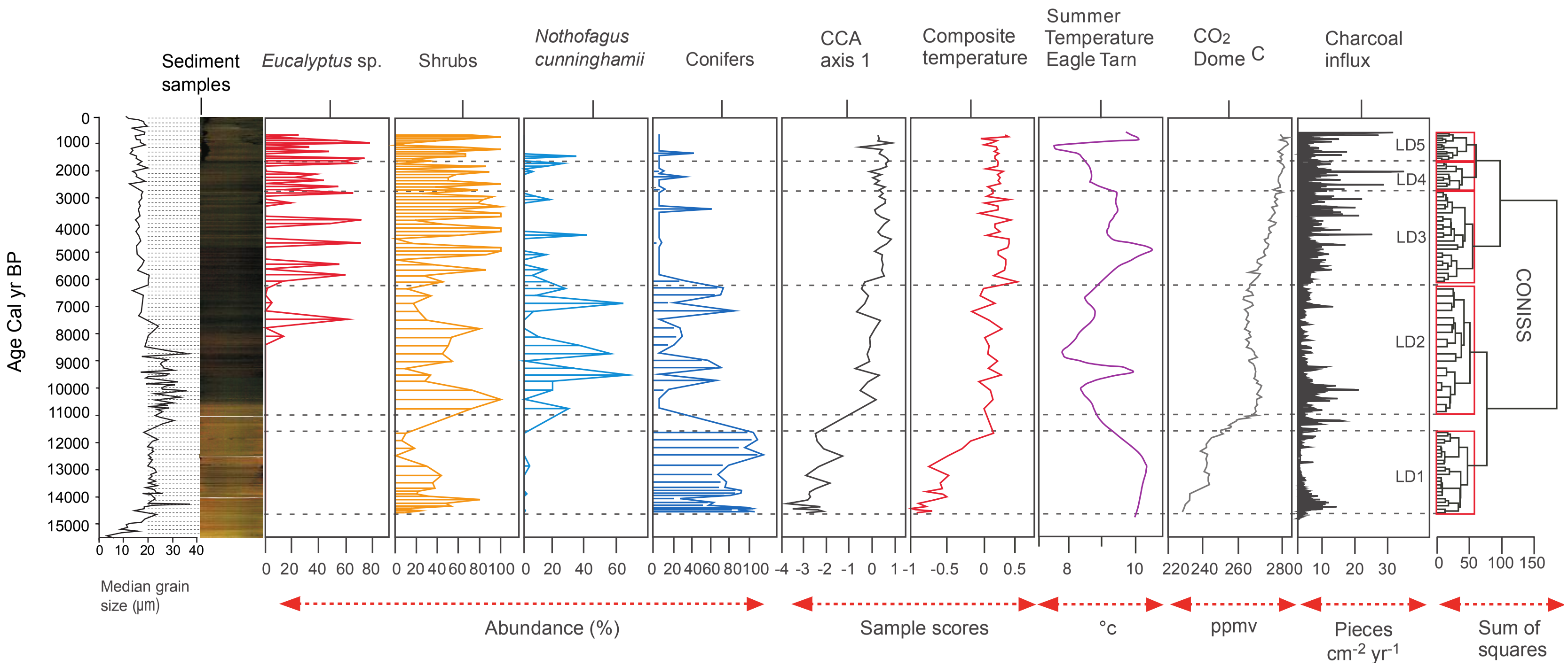

Figure 3-2 Stratigraphic sequence of sediments from Lake Dobson showing median grain size (Rees & Cwynar Unpublished), and sediment samples taken every ten centimetres (grey lines). Main plant macrofossil types are shown according to stratigraphic age, and associated environmental stages. Sample scores on CCA axis 1 for the plant macrofossil represents the changes in vegetation occurred for the last 15 cal kyr BP due to environmental factors (temperature, carbon dioxide, and the influx of charcoal) providing a background for the interpretation of the vegetation shifts. Stratigraphic zones described in section 3.5.1.

After a gap of *c*. 900 yr from 11.8 to 10.9 cal kyr BP, a major plant transition is recorded in the early Holocene of zone LD2 (680–515 cm; 10.9–6.3 cal kyr BP). A sharp drop in the representation of alpine conifers, from an average representation of 72% in zone LD1, to 27% is recorded. The rainforest tree *Nothofagus cunninghamii* increases its representation in this zone to an average of 23% with a maximum representation peaking around 9.5, 8.8, and 6.8 cal kyr BP. Trace amounts of other rainforest species such as *Phyllocladus aspleniifolius* (9.3 cal kyr BP), are also recorded during this period. Towards the top of the boundary *Eucalyptus* and *Leptospermum* begin to make an appearance in the record, albeit in small percentages. Additionally, the bryophyte flora indicates the presence of species that are today characteristic of cool temperate rainforest, and moist/shaded environments, such as the leafy liverwort *Leptoscyphus* (9.8–7.4 cal kyr BP) and the mosses *Camptochaete arbuscula* and *Weymouthia spp*. (Table 5-2, Fig. 3-2).

The lower boundary of zone LD3: 515–295 cm (6.3–2.7 cal kyr BP) is characterised by a decline in the representation of *Nothofagus cunninghamii* and alpine conifers. In contrast, the upward increase of *Eucalyptus* and other shrub species, especially *Leptospermum*, *Epacris serpyllifolia*, and *Bauera rubioides* likely represents the definitive establishment of the subalpine *Eucalyptus* open woodland that is now dominant around Lake Dobson (Fig. 3-3). Fossil mosses document the decline of species that characterised the rainforest stage (Fig. 3-2), while other species such *Sphagnum*, and *Pyrrhobryum* become dominant.

Eucalyptus continues to increase their representation in zone LD4: 28–180 cm (2.5–1.2 cal kyr BP) reaching an average value of 36%, while the average value of shrub species —*Epacris serpyllifolia* and *Bauera rubioides*— dropped to 49%. *Nothofagus* *cunninghamii* is recorded only in the upper boundary of this zone with around 5% representation. A small peak of alpine conifers (2.5%) is recorded in the middle part of the section.

Zone LD5 (50–180 cm; 1.2 cal kyr BP–340 cal yr BP) archives a relatively low number of plant macrofossil remains, preventing an exhaustive description of this layer. However, the vegetation signal is similar to that of zone LD4, and is mainly characterised by the dominance of *Eucalyptus*/*Epacris serpyllifolia,* although *Nothofagus cunninghamii* is not recorded.

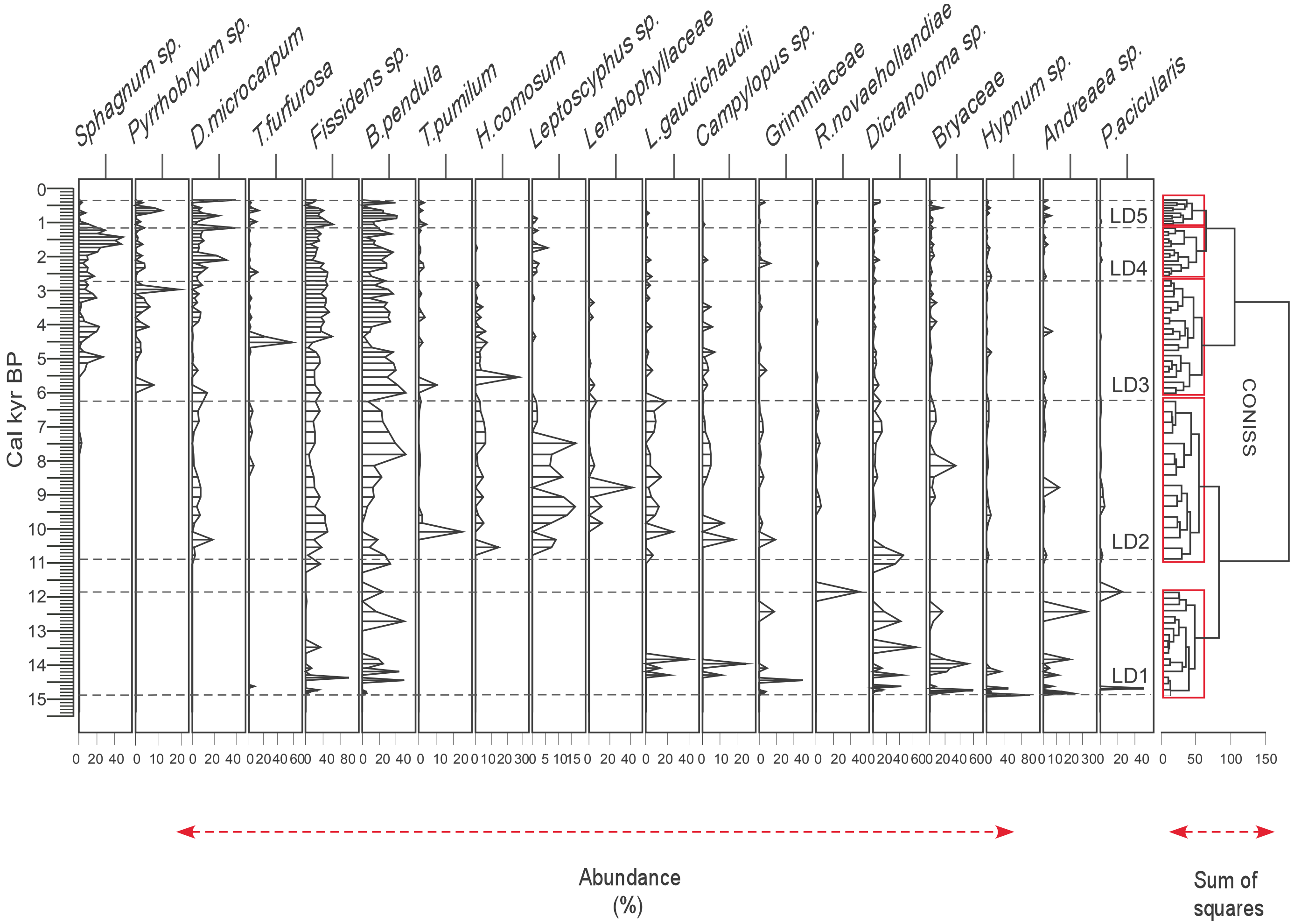

Figure 3-3 Summary diagram of the main bryophytes species (% abundance) recorded in the plant macrofossil record from Lake Dobson.

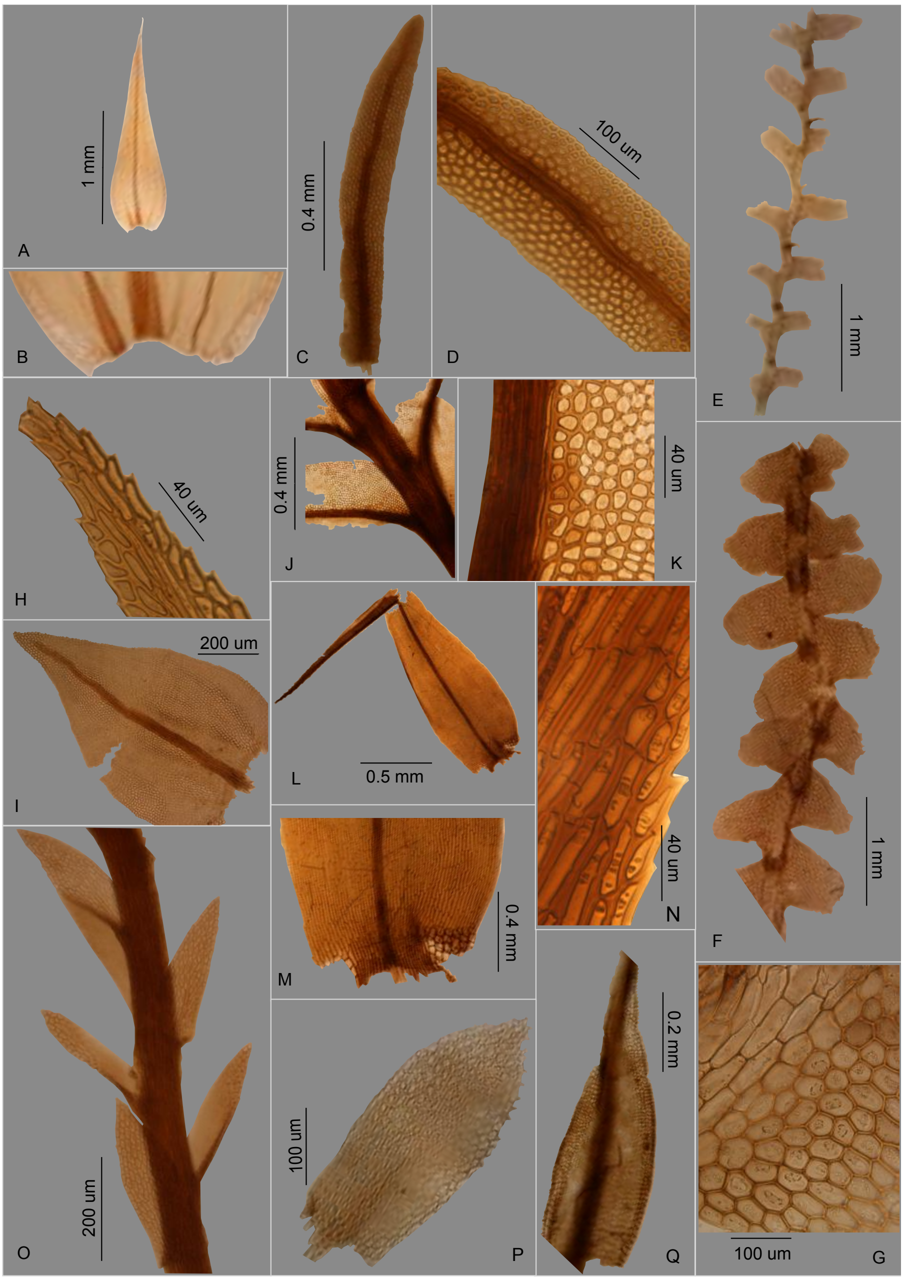

Figure 3-4 Selected fossil bryophytes from the sediments of Lake Dobson. A-B *Breutelia pendula*: leaf outline and allar cells at the base of the lamina. C-D *Fissidens sp*. leaf and mid lamina cells. E-G Stem fragments of the liverwort *Leptoschiphus* sp. and leaf cells. H-I *Tuidosis furfurosa* leaf outline and apex. J-K *Leptotheca gaudichaudii* leaf outline, and midleaf cells and costa. L-N *Dicranoloma sp*. leaf outline, leaf base and cells of the leaf margin. O-P *Thamnobryum pumilum* stem fragment and leaf. Q *Andrea australis* leaf.

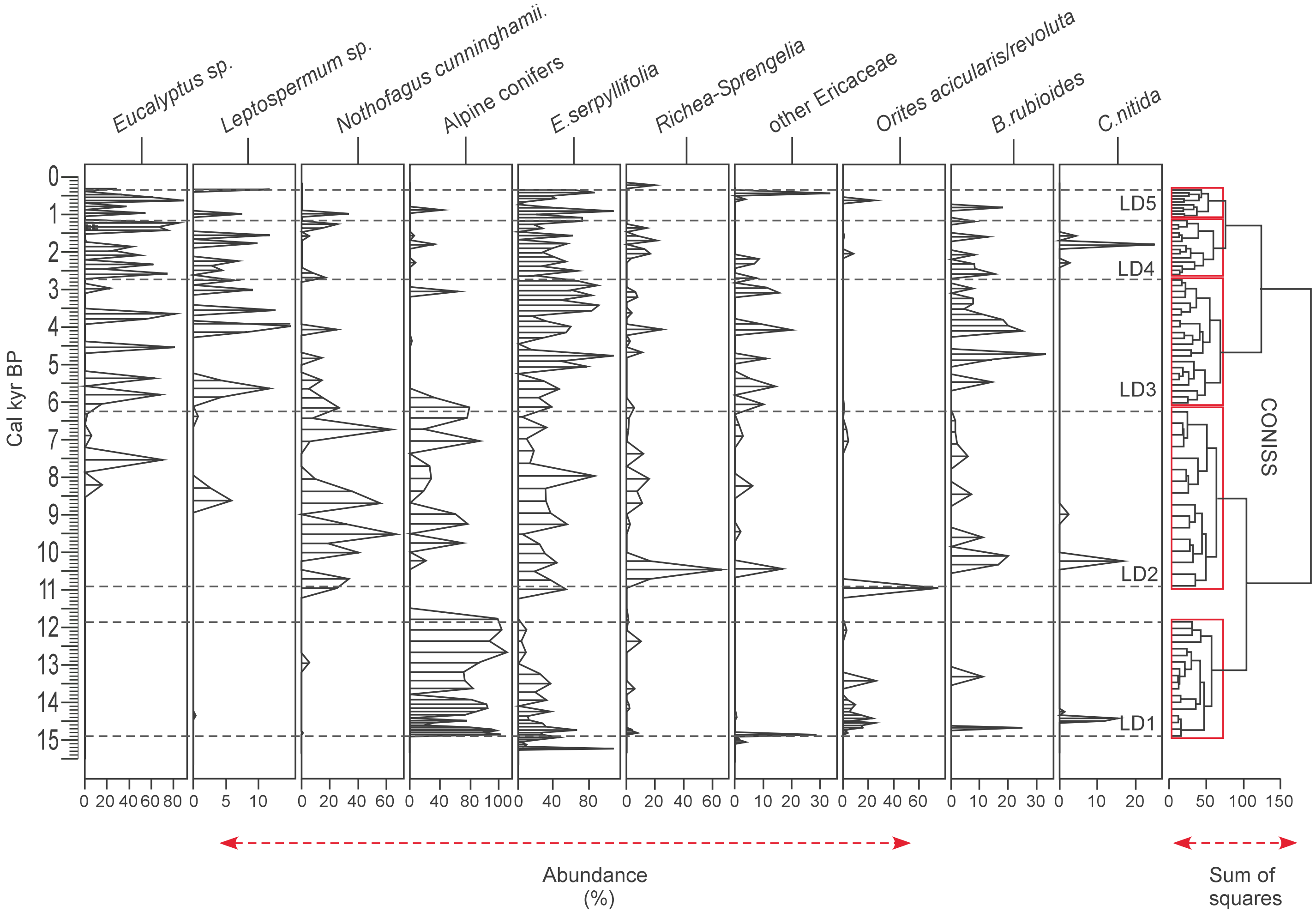

Figure 3-5 Summary diagram of the main vascular plant types recorded as plant macrofossils from Lake Dobson according to stratigraphic age.

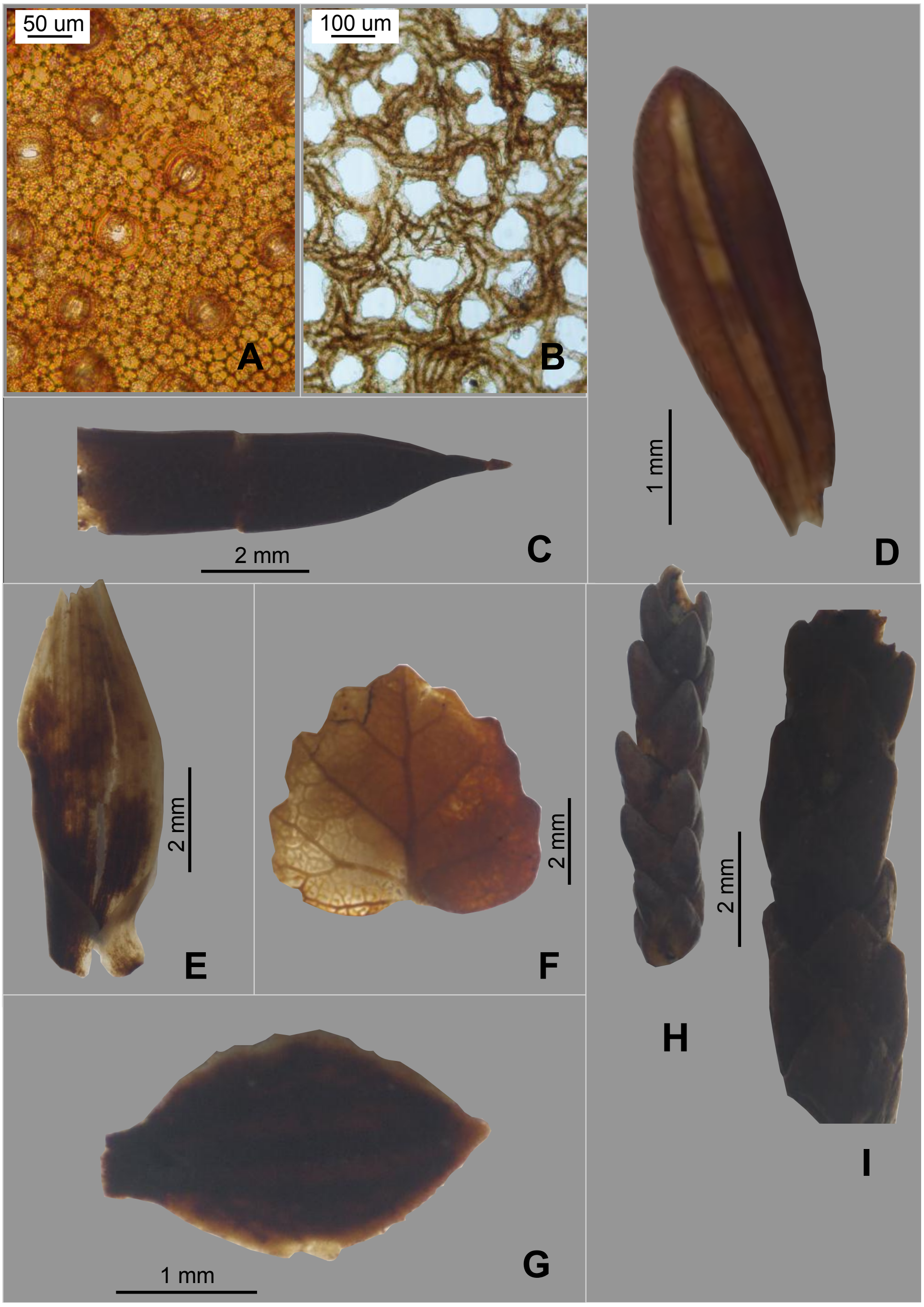

Figure 3-6 Selected vascular plant remains recorded in the sediments of Lake Dobson. A-D Proteaceae: (A) hypodermis, (B) leaf cuticle , and (C) leaf of *Orites acicualris*; (D) *Orites revolutus* leaf. (E) *Sprengelia incarnata* leaf. (F) *Nothofagus cunninghamii* leaf. (G) *Epacris serpyllifolia* leaf. H-I Cupressaceae, stem fragments with leaves: (H) *Diselma Archeri*, (I) *Athrotaxis cupressoides*.

3.5.2 Gradient analysis

Unconstrained ordination (DCA) of the plant macrofossil data based on log-transformed data showed a first axis explaining about 12% of the total variance (λ=0.33), and a gradient length of 2.7 standard deviations along the first ordination axis (Fig. 7-2 in Appendix 2). According to the criteria of Borcard et al. (2011) and Legendre and Birks (2012), this value makes CCA appropriate for identifying environmental associations with the macrofossil data. Overall, DCA axis 1 highlights the contrast between the dominance of alpine vegetation during the Lateglacial, and rainforest and open woodland vegetation during the early and mid-Holocene. Negative species scores indicate cool-adapted high alpine/subalpine and fire sensitive plant taxa, which were present mainly in the Lateglacial samples before 11.5 cal kyr BP. Positive species scores, on the other hand, were produced by species that characterised *Eucalyptus* open woodland vegetation, while plant species displaying intermediate values represent the rainforest stage.

3.5.3 PCA and composite temperature curve

PCA axis 1 explained 72% of the variance in the temperature data. It was therefore assumed that PCA axis 1 is a good representation of mid-high southern latitude trends in temperature for the last ~15000 years (see Fig. 3-2 and 7-2 in Appendix 2).

3.5.4 CCA of plant macrofossils and environmental variables

CCA of the full data set of predictors and response variables produced a statistically significant model (P = 0.001 after 999 permutations) with composite temperature, carbon dioxide, and charcoal as independently significant variables. The independence of the variables was assessed with the variance inflation factor (VIF), which was fewer than five for the three variables. Forward selection and parsimonious CCA identified the same three environmental variables as predictors of changes in vegetation. These three environmental variables explained 16% of the total variability in the plant macrofossil data, while canonical axes 1 and 2 explained 89% of the constrained variability (Table 7-3 in Appendix 2).

The first axis of the CCA site scores is correlated with CO_2 and temperature, while the second axis correlates with fire (Fig. 3-5). Overall, the CCA biplot suggests that sample sites in the left hand side of the perpendicular line to temperature contain species that prefer higher than average temperature and CO_2 for the period i.e. most of the rainforest and open woodland species, comprising sites 1–60 (age range ~350 cal BP to 10.1 cal kyr BP). Sample sites 63–80 (age range 14.5–10.8 cal kyr BP), situated on the right hand side of the perpendicular, contain high subalpine/alpine plant species preferring lower than average temperature and CO_2 levels for the period. Plant species and sample sites on the bottom left part of the plot seem to have affinities to fire-prone environments (Fig. 3-5).

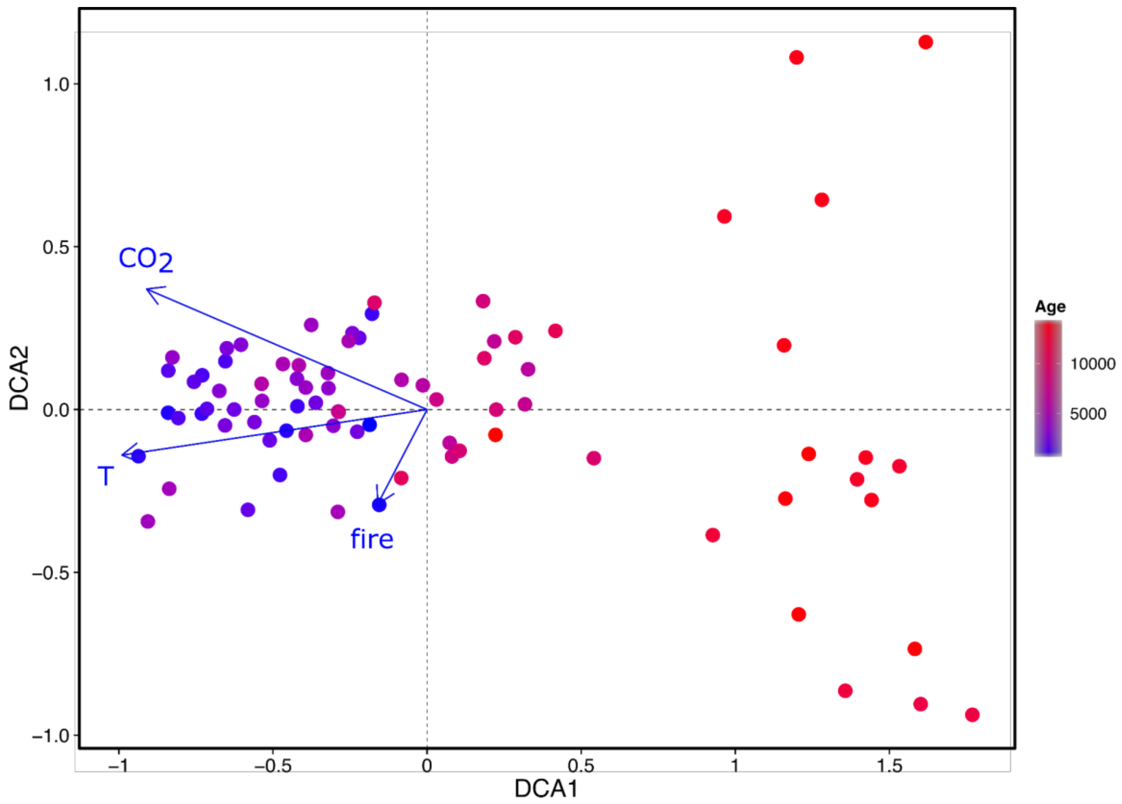

Figure 3-7 DCA ordination plot of the plant macrofossil assemblages from Lake Dobson with significant environmental (temperature, carbon dioxide and charcoal influx) variables superimposed

3.6 Discussion

The early presence in sediments of conifers and angiosperm heath shrubs species suggests that alpine/plant communities assembled from local survivors at the Last Glacial-interglacial transition. However, the delayed postglacial arrival of other plant species, especially *Eucalyptus*, around the early middle-Holocene boundary (~8.1 cal kyr BP) indicates later immigration from lowland areas.

3.6.1 Evidence for local glacial survival

The presence of high subalpine/alpine plant species (i.e. the alpine conifers: *Athrotaxis cupressoides*, *Microcachrys tetragona*, *Diselma archeri*, *Pherosphaera hookeriana,* and sclerophyllous heath shrubs: *Orites revolutus*, *Orites acicularis*, *Epacris serpyllifolia*) in the oldest macrofossil-bearing sediments in the Lake Dobson core before 14.5 cal kyr BP (Fig. 3-2) argues for the glacial survival of these plants near Lake Dobson. In particular, the plant macrofossil evidence indicates that these plants were part of the vegetation around Lake Dobson by 14.9 cal kyr BP (Fig.3-2) shortly after the deglaciation was completed ~16 000 cal BP (Mackintosh et al. 2006). Although Lake Dobson itself was glaciated during the LGM, unglaciated areas occur as close as 200 m from the lake (see Fig. 2 in Mackintosh et al. 2006), including north-east facing slopes that may have provided relatively warm and sheltered microsites for the survival of woody plants. The early local establishment of alpine vegetation in the area is supported by a pollen-based vegetation reconstruction at Eagle Tarn, which lies in the vicinity of Lake Dobson (Fig. 3-1) providing additional evidence of a proximal alpine community around the same time (12 800–12 000 14C years BP; Colhoun 1996).

The possibility of upslope transport of plant remains seems unlikely as an explanation for the early representation of species in the sediments of Lake Dobson, even though such transport has been recorded for modern leaves of *Dryas*, *Salix* and *Vaccinium* in Alaska (Glaser 1981). Unlike the light, deciduous leaves from the Alaskan study, the relevant macrofossil remains at Lake Dobson are heavy (whole conifer shoots and evergreen leaves) and likely to be of local origin (see Chapter 2). In addition, at least for the alpine conifers, the plant remains in sediments before 14.5 cal. kyr BP are likely to be locally derived because of their high frequency in the sediments (11–177 leaves).

Survival through the LGM would involve persistence under conditions that appear to be inconsistent with the current bioclimatic ranges of some of the species, especially *Athrotaxis cupressoides*, which only extends marginally above the treeline across its current range. Paleotemperature reconstructions based on fossil pollen and estimations of lapse rates for cirque initiation indicate temperatures of ~ 5–8°C below modern values for the LGM in western and central Tasmania (Colhoun and Van De Geer 1986a; Colhoun 2000; Colhoun et al. 1999; Mackintosh et al. 2006). Applying a temperature decrease of 5°C in the Lake Dobson area and an altitudinal thermal lapse rate of 0.006 °C m^{-1} would predict treelines approximately 900 m below its current position, leaving a completely treeless area of at least a 20 km radius around Lake Dobson (Fig. 3-1). A less dramatic degree of cooling for the LGM of as little as 3.7–4.2 degrees has been proposed (Barrows and Juggins 2005; Fletcher and Thomas 2010), but even under these models Lake Dobson is likely to have been distant, ~ 8–10 km, from the treeline. Such survival could be due to the occurrence of non-analogue environments during the period, a failure of the species to occupy its full climatic niche and/or changes in physiological tolerance —i.e. evolutionary changes in the fundamental niche (e.g. Worth et al. 2014). In contrast, it is unclear whether LGM climates were within the current ranges of the other proposed glacial survivors (the conifers *M. tetragona*, *D. archeri*, *P. hookeriana* and the alpine/subalpine angiosperm shrubs from Ericaceae and Proteaceae). The lower thermal limits of these species are poorly understood because the species now extend to the highest altitude (coldest) points in Tasmania. However, significant drying of climates during the LGM (Bowden 1983; Bowler 1976; Duller and Augustinus 2006; Galloway 1965; Jackson 1999; Petherick et al. 2013) may have stressed these species, which are today restricted to mountain areas of relatively high precipitation.

The alternative explanation to local glacial survival, fast upward migration rate, is unlikely considering that all the alpine conifers, with the possible exception of the bird-dispersed species *M. tetragona*, have very low dispersal abilities (Cullen and Kirkpatrick 1988b; Kirkpatrick and Dickinson 1984). The low dispersal capacities of the conifers are further exacerbated by the infrequent production of seeds (e.g. *Athrotaxis* mast seeding every 6 years), and a period of ~100 years before plants are mature enough to set seeds (Cullen and Kirkpatrick 1988b; Ogden 1978).

Similar dispersal constraints have been observed in *Nothofagus cunninghamii* (Hickey et al. 1982; Howard and Ashton 1973; Kirkpatrick and Dickinson 1984; Kirkpatrick and Fowler 1998; McKenzie 1997; Read and Hill 1985a; Tabor et al. 2007; Worth et al. 2009). Therefore, its early appearance in the plant macrofossil record is also difficult to explain by a fast upward migration rate —seed dispersal rates under current dispersal conditions are conspicuously slow (Jordan 2003). *Nothofagus cunninghamii* has a low and sparse representation in early parts of the plant macrofossil-bearing sediments from Lake Dobson (14.8 and 13.1 cal kyr BP) when temperature and CO_2 were still low (Fig. 3-2). Alternatively, the rapid postglacial expansion of *N. cunninghamii* at the start of the Holocene (~10.9 cal kyr BP), after maximum temperature values were reached (~11.8 cal kyr BP), would argue for the proximity of the species in small patches or isolated individuals in areas near the lake remaining invisible to the pollen record. The local survival of *N. cunninghamii* in montane areas near Lake Dobson seems credible, especially considering its very low rates of seed dispersal (Hickey et al. 1982) and genetic evidence of slow post-glacial migration (Worth et al. 2009). This inference of unexpected glacial survival of *N. cunninghamii* at high altitudes is reinforced by DNA chloroplast phylogeographic evidence showing a suite of rare haplotypes restricted to montane locations above 800 m in south and western Tasmania (Worth et al. 2009). Overall, distribution modelling combined with genetics have provided strong evidence for survival of this species in climates considerably colder and drier than those the species now occupies (Worth et al. 2014).

3.6.2 The time lag in migration of Eucalyptus

The late appearance of *Eucalyptus* in the plant macrofossil record from Lake Dobson contrasts with pollen studies at similar altitude sites in southern Tasmania. These studies have been used to infer that *Eucalyptus* reached Eagle Tarn, only 200 m from Lake Dobson (Fig. 3-1) shortly before 11.5 cal kyr BP (10 000 14C yr BP; Colhoun 1996; Macphail 1979; Markgraf et al. 1986). The discrepancy between pollen and plant macrofossil evidence may reflect a taphonomic bias in pollen representation. Uphill wind transport of pollen from trees that are abundant at low altitudes can lead to high abundance of these pollen types in treeless alpine Lateglacial environments (Barnekow, 1999; Birks and Birks, 2008; Birks, 2003; Birks and Birks, 2000; Wick et al., 2003). Such patterns can easily be misinterpreted as local appearance of these lowland species. The absence of macro-remains for *Eucalyptus* in Lateglacial-early Holocene sediments cannot be explained by low preservation potential or misidentification, since such remains are consistently present in the record after 8.1 cal kyr BP and are abundant in recent assemblages (Chapter 2).

A time lag caused by slow postglacial dispersal from lowland refugia rather than local glacial survival may help explain the late establishment of *Eucalyptus* in the vegetation around Lake Dobson. Particularly, the plant macrofossil record suggests that the modern configuration of the vegetation that characterises the subalpine/treeline areas in Mt. Field —i.e. *Eucalyptus* open woodlands— was not reached before the early middle-Holocene boundary ~8.1 cal kyr BP. Importantly, a hypothesis of slow uphill migration is consistent with the low dispersal capabilities typical of *Eucalyptus* species (Jordan 2003; Potts 1990; Shaw et al. 1984) and molecular evidence supporting the survival of eucalypts in multiple lowland glacial refugia (McKinnon et al. 2004; Nevill et al. 2008; Nevill et al. 2010) across eastern Tasmania, and subsequent expansion into formerly glaciated areas following the ice retreat (Byrne, 2008; McKinnon et al., 2004).

Eucalypts present a number of traits that have been linked to fire —e.g. volatile oils present in the leaves, and slow decomposition rate of the litter (Gill 1997; Tng et al. 2012). However, from the results presented in this study it seems likely that the delayed arrival of *Eucalyptus* to the subalpine area of Lake Dobson was not constrained by lack of fire or to unsuitable climates, because charcoal is recorded throughout the sediment profile, and temperatures became suitable at least 4000 years before the genus appears in the record (Fig. 3-2). Additionally, the relevant species of

Eucalyptus have wide tolerances of precipitation including climates both considerably wetter and drier than those currently at Lake Dobson. Thus, the lag in migration of *Eucalyptus*, and subsequent expansion into the Lake Dobson area may have been constrained by the distance from lowland areas of refugia, possibly with a contribution of competition from the existing species in the area.

3.6.3 Plant macrofossils abundance versus environmental trends

Although the early presence of cold adapted species (i.e. alpine conifers and high alpine/subalpine shrubs species) imply that some species re-established near Lake Dobson from local sources, the abundance of macrofossils of these species follows climatic trends as well (Fig. 3-2). In particular, the representation of alpine conifers remains relatively high until the Lateglacial-Holocene transition ~11.8 cal kyr BP, period after which alpine conifers disappear from the record for ca. 2000 years followed by the appearance of *Nothofagus cunninghamii* around 10.9 cal kyr BP. The highest abundances of *N. cunninghamii* is recorded at *c*. 10–8.5 cal kyr BP (Fig. 3- 2), which is in close agreement with the inference of an early postglacial climatic "optimum" based on pollen studies in Tasmania (Colhoun 1996; Macphail 1979; Markgraf et al. 1986). The presence of a climatic optimum is also supported by the co-occurrence in the plant macrofossil assemblages of other temperate rainforest species such as *Phyllocladus aspleniifolius*, *Athrotaxis laxifolia* and mosses, although it is highly unlikely that any extensive area of dense rainforest developed in the area (Fig. 3-2 and Fig. 3-3). Thus, the abundance of local survivors may represent climate well, even though species dependent on immigration (such as *Eucalyptus* species) may show strong climatic lags (Fig. 3-2).

3.7 Conclusion

The use of plant macrofossil assemblages in vegetation studies may provide additional information to that derived from fossil pollen grains and spores. Particularly, plant macrofossil evidence confirming the local presence of species is required in situations in which pollen and molecular studies provide contradictory inferences. Specially, macrofossils may be particularly useful in determining the location of glacial refugia, and in circumstances in which the low local pollen production of the vegetation (e.g. treeline environments during the LGM and Lateglacial) may result in the misleading interpretation of high percentages of long-distance transported pollen types.

The plant macrofossil record from Lake Dobson in subalpine south-central Tasmania provides complementary information to pollen-based vegetation reconstructions for the area. Importantly, plant macrofossil assemblages provide refined information for understanding the sequence of postglacial assembly of the vegetation near the treeline during a critical period of climate change. In particular, they support the local glacial survival for poorly dispersed plant species such as the alpine conifers, and *Nothofagus cunninghamii*, although it also provides evidence for the delayed mid-Holocene appearance of *Eucalyptus*.

Thus, plant macrofossil evidence presented in our study strongly supports the view that plant species may display individual responses to face environmental changes, and that such responses are indeed contingent to the specific adaptations, dispersal limitations, and physiological capacity to tolerate climatic extremes (Huntley 1991; Stewart et al. 2010; Williams 2009).

4 Chapter 4 – Seeing the forest from the leaves: Using leaf traits of *Nothofagus cunninghamii* to estimate forest structure

4.1 Abstract

The potential to characterise the structure of the past vegetation through the anatomy of leaves has not been yet extensively assessed. In particular, leaf characteristics such as stomata and vein density respond to several environmental variables (e.g. temperature and atmospheric carbon dioxide), and leaves at different levels in a canopy also respond to a gradient in microenvironmental conditions such as light intensity and water demand. This study analyses variation in vein and stomatal density, and leaf size in foliage and litter leaves of *Nothofagus cunninghamii* to assess whether it is possible to discriminate between open and closed forest.

Overall, closed canopy leaves have lower vein densities relative to stomatal density compared to open canopy leaves especially, once differences in leaf size are taken into account. The effect of leaf size in the relationship of veins and stomata is important, because it means that these characteristics can be used as proxies even if they have been affected by leaf shrinkage in the process of fossilisation. Additionally, it was found that the mean size and stomatal characteristics of litter leaves are biased towards those of canopy leaves, presumably because of greater production of canopy compared to subcanopy leaves. Estimation of forest structure is therefore not straightforward, and would require higher sampling intensity to capture the signature of subcanopy leaves. These constraints may also apply to the fossil record

considering it generally accepted that, typically, more canopy leaves are incorporated in fossil assemblage than shade leaves.

4.2 Introduction

An important aspect to understanding the ecology of prehistoric vegetation is whether fossil plant communities were open shrublands or closed forest, and alpine treelines in particular represent one of the most important types of transition between forest dominated environments to open vegetation (Körner 1998). There has been increasing interest in using fossil proxies to assess this key aspect of plant community structure (Carcaillet and Thinon 1996; Carnelli et al. 2002; Jordan et al. 2014; Shiyatov 2003; Tinner et al. 1996). Plant macrofossils, especially leaves, can be useful tools to address such questions (Birks 2007; Tinner and Theurillat 2003).

Typically, variations in stomatal density, leaf size, and vein density have been used to investigated the evolutionary history of land plants and past climate conditions (e.g. Brodribb et al. 2009; McElwain and Chaloner 1995; Uhl and Mosbrugger 1999), and have been linked to differential light intensities through the canopy (e.g. Eschrich et al. 1989; Onwueme and Johnston 2000; Poole et al. 1996). These studies have generally demonstrated that within species, sun leaves usually have higher stomatal and vein density than shade leaves and are often smaller (Boyce 2009; Carins Murphy et al. 2012; Dickison 2000; Givnish 1988; Kürschner 1997; Sack et al. 2006; Uhl and Mosbrugger 1999). However, this differentiation of sun v. shade leaves through the canopy also represents a gradient in the leaf-to-atmosphere evaporative gradient (Zwieniecki et al. 2004). Furthermore, several studies have established that maximum photosynthetic performance in leaves is constrained by a balance between the demand for water —created by the transpiration of water through stomata— and the supply of water through the vascular system (Carins Murphy et al. 2012; Zwieniecki et al. 2004). The investigation of *Nothofagus cunninghamii* leaves in a previous study have provided important evidence of coordination between leaf hydraulic conductance (determined largely by the leaf venation density) and maximum stomatal conductance (determined by stomatal density) under the contrasting conditions of evaporative demand that characterise sun and shade leaves (Brodribb and Jordan 2011; Fig. 7b). However, it is not clear whether this sun and shade response can form the basis for predicting canopy structure.

Crifò et al. (2014) proposed that vein density is a good indicator of the position of leaves within canopies, and therefore vein density of fossils may provide a useful tool for investigating the structure of past forests. However, Crifò et al. (2014) made no consideration of the difference between open and closed vegetation. In addition, several factors complicate the relationship between vein density and vegetation structure. Firstly, vein density varies not only from species to species (Brodribb et al. 2010; Sack et al. 2012; Uhl and Mosbrugger 1999), but also among populations of species (e.g. Brodribb and Jordan 2011). Secondly, changes in leaf size during fossilisation, for instance shrinkage (Blonder et al. 2012; Cleal and Shute 2007; Jordan 2011), can create biases in the estimation of vein density. However, biases caused by shrinkage will also be apparent in leaf size and stomatal density (Cleal and Shute 2007). Therefore, allowing for the effects of leaf size and stomatal density in comparisons of vein density may be useful tool for reconstructing the structure of the vegetation from fossil leaves.

This chapter explores the potential for leaf macrofossils to identify forest structure (i.e. closed forest versus open vegetation) using contemporary leaves (i.e. canopy and litter leaves) from a montane forest population of the evergreen tree species *Nothofagus cunninghamii* (Hook.) Oerst. This species is particularly suitable for such investigations because it is known to show substantial anatomical variation in response to sun and shade (Brodribb and Jordan 2011; Hovenden and Vander Schoor 2006), and is well represented in fossil assemblage back to at least to the early-middle Pleistocene in Tasmania (Jordan and Hill 1994). *Nothofagus cunninghamii* is endemic to south-eastern Australia, and is the main component of cool temperate rainforests that currently dominated the wettest parts of Tasmania (Howard and Ashton 1973). It presents a wide altitudinal range from sea level to around the treeline (Hovenden and Brodribb 2000), and ranges in size from a 50 m tall tree to a short shrub at the higher limit of its distribution (Worth et al. 2009). In addition, the genus *Nothofagus* is an important component of both modern and fossils floras from mid to high-latitude areas of the Southern Hemisphere (Hill and Jordan 1993; Hill et al. 2015).

This chapter focuses particularly in the use of leaf trait variation —i.e. leaf size, vein density, and stomatal density —from a montane forest of *Nothofagus cunninghamii* to assess whether, there is an open versus closed canopy signal in the leaves. In addition, this study examines whether canopy structure can be predicted from the forest floor litter. Finally, a short case study is presented using Holocene leaf fossils of *Nothofagus cunninghamii* from Lake Dobson, central Tasmania.

4.3 Material and methods

4.3.1 Plant material

In the present study, canopy and sub-canopy leaves of *Nothofagus cunninghamii* were collected from a population in the subalpine vegetation zone around Lake Dobson (42°41.0S, 146°35.4E; 1034 m a.s.l.) in Mt. Field National Park south-central Tasmania (Fig. 3-1). From this population five-isolated 'open forest' trees, and five 'closed forest' individuals were sampled along the Pandani Grove Natural Walk track (Fig. 2-1). From each tree, two branches from the upper canopy and lower canopy were collected. Five arbitrarily located samples from the forest litter from each forest canopy type were collected, and pooled to create a representative sample for each forest canopy type. Fifty leaves per canopy type were randomly selected—i.e. five sun and five shade leaves from each open and closed canopy tree—alongside with 20 leaves from each open and closed litter type from under sampled trees (litter samples pooled together for open and closed canopy.

The fossil leaves of *Nothofagus cunninghamii* were extracted from the sediments of Lake Dobson (see Chapter 3). Only three of the sediment samples had sufficient (≥5) complete or near complete leaves to provide an adequate sample. These sediment samples corresponded to three dated intervals of early and mid-Holocene ages (~ 9.3, 6.8 and 6.3 cal kyr BP; 17 leaves).

4.3.2 Sample preparation and measurements

Leaf area was determined for all leaves using a flatbed scanner (resolution 300 dpi) and the image analysis program ImageJ (National Institutes of Health, Bethesda, MD, USA). After leaf area determination, each leaf was divided in half and a paradermal section was prepared from one half to allow measurements of vein density (VD), and a cuticle preparation from the other half to allow measurement of stomatal parameters.

Paradermal sections were prepared by removing the upper epidermis and palisade tissue with a sharp razor. Sections were placed in commercial household bleach (50 g L^{-1} sodium hypochlorite and 13 g L^{-1} sodium hydroxide) until all pigment was removed and the section was clear. Sections were then rinsed, stained (1 % toluidine blue), and mounted on microscope slides using phenol glycerine jelly. Vein density was estimated from photomicrographs of three fields of view 10x magnification (approximately 1.9mm^2) placed near the apex, base and central part of the leaf avoiding midribs and margins. Photomicrographs were taken using a Nikon camera (DS-L1; Melville, NY, USA) mounted on a Leica microscope DM 1000; Nussloch, Germany. Total vein length for each field of view in mm was determined using ImageJ, and the density of veins as the total vein length divided by field of view area.

Abaxial cuticle sections (*N. cunninghamii* is hypostomatic) were prepared from the remaining half leaves by removing some of the paradermal tissue with a sharp razor and then soaking in warm 10% aqueous Cr_2O_3 until clear. Sections were rinsed thoroughly, stained (crystal violet < 0.1%), and then mounted on microscope slides using phenol glycerine jelly.

From all cuticle preparation, photomicrographs from four fields of view at 20x magnification (fov_{area} = 0.04 mm^2) were taken to count the numbers of stomata (SN) and epidermal cells (EN). These parameters were used to estimate stomatal density (SD = SN/fov_{area} mm^{-2}, and stomatal index (SI = SN/(SN+EN) x 100 mm mm^{-2}).

4.3.3 Statistical Analysis

Linear regression implemented using the LM function in R (R Team 2015) was used to relate differences in vein density between open and closed forest, and between litter types. There was significant variation among trees in the foliage data for all variables, and therefore statistical analyses for the foliage data was based in tree means. Following, linear regression was applied starting with the full set of variables including two and three-way interaction between the factors (forest and exposition) and covariates (stomatal density and leaf area). The model selection was performed using the 'drop1' (model, test = "F") command of the *stats* package in R (R Team 2015). This selection model approach is based on dropping the least significant term one at a time, and refitting the model until all remaining terms are significant. The *multcomp* package in R (Bretz et al. 2010) was used for pairwise comparisons when deemed necessary.

Because direct comparison of litter and foliage leaves was precluded by the strong tree effect, probability density functions were calculated for the comparison of forest and litter data using the 'density' function in R (R Team 2015). Analysis of covariance (ANCOVA) was used to test for equality of the slopes and to assess whether the relationship of the regression parameters was the same regardless of forest structure.

4.4 Results

4.4.1 Canopy versus sub-canopy leaves

Canopy leaves were smaller and had higher densities of veins and stomata than sub-canopy leaves (Fig. 4-1). There was a significant overall relationship between the position of the leaf in the crown and VD ($R^2 = 0.55$; $P < 0.01$), although the highest variation in VD occurred between the two forest populations rather than within forest. Specially, canopy and sub-canopy leaves from the open forest had consistently higher VD (12-14%, $P < 0.05$ in both cases) compared to closed forest, although SD and LA were non-significantly different either between or within forests. However, differences in leaf parameters were especially high between the two canopy extremes (open-sun v. closed-shade). Thus, canopy leaves from the open forest had around 20% higher vein density ($P < 0.001$), 26% more stomata ($P < 0.05$), and were about one-fourth the size of shade leaves from the closed forest ($P < 0.05$; Fig. 4.1).

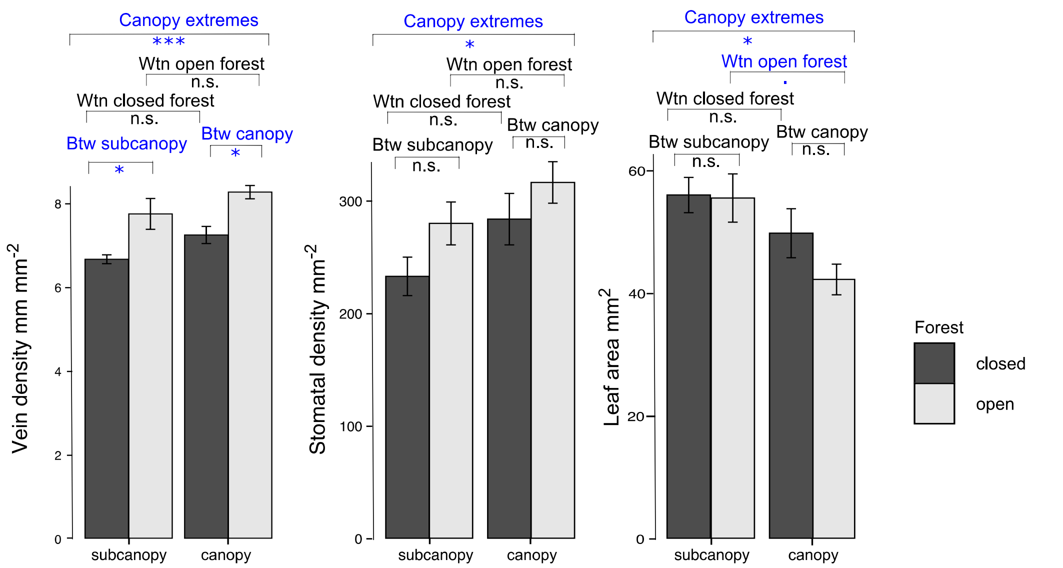

Figure 4-2-1 Differences in mean values of vein density, stomatal density, and leaf size (± SE) comparing sun-canopy (shade-subcanopy) leaves between the two forest types, sun and shade leaves within open forest (closed forest), and between the two forest extremes (open-canopy and closed-subcanopy leaves). Significance codes: *** = $P < 0.001$; * = $P < 0.05$; n.s. = $P > 0.05$.

4.4.2 Closed forest versus open forest

There was a strong overall relationship between VD and forest structure ($R^2 = 0.46$; $P < 0.001$). In particular, leaves from the open forest had 13% higher VD, although the individual values of SD and LA did not differ significantly between the two forests. However, fitting the linear regression with both stomatal and vein density indicated that leaves from the open forest had significantly higher density of veins for a given number of stomata compared to closed forest leaves ($P < 0.001$; $R^2 = 0.66$). This relationship was further improved when fitting the full model including leaf area ($P <$

0.001; R^2 = 0.73; Fig. 4-2). The ANCOVA analysis suggested that the slope of the relationship was the same regarding forest structure.

Moreover, regression lines fitted individually for open and closed canopy indicated that the regression of leaf size on vein density in open forest was displaced upwards compared to closed canopy ($P < 0.001$; $R^2 = 0.82$) than open canopy leaves, whereas stomatal density had a significant effect among open canopy leaves ($P < 0.01$; $R^2 =$ 0.55).

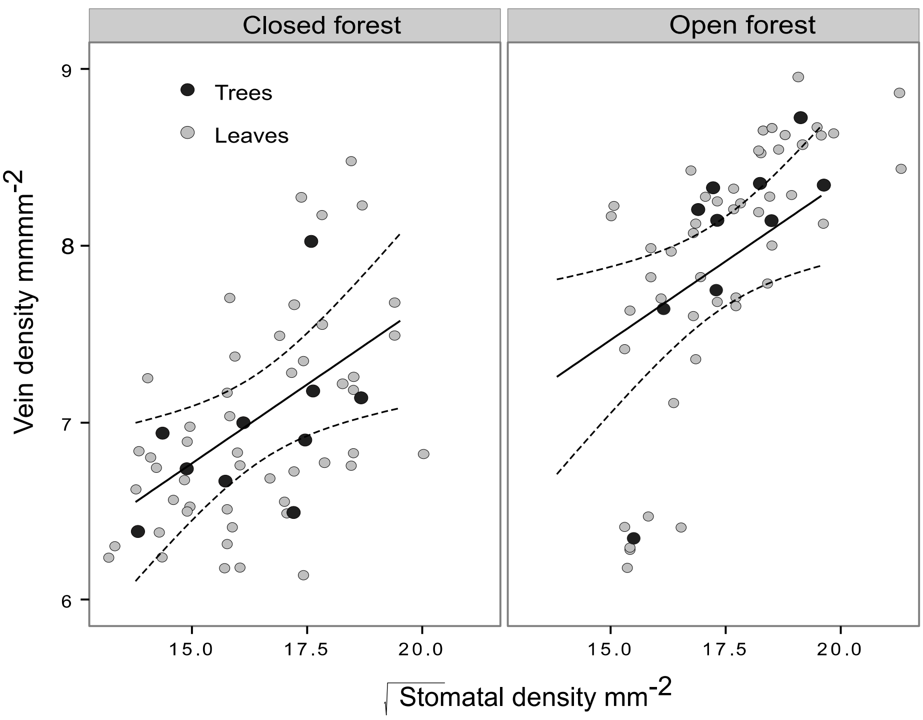

Figure 4-3-2 Open and closed canopy vein density and √stomatal density values of *Nothofagus cunninghamii* (R^2 *adj.* = 0.73; $P < 0.001$) when leaf area is centred to its mean overall value (51.2 ± 9.1 SD).

4.4.3 Differences between litter assemblages

Although direct comparison of litter and foliage leaves was precluded by the strong tree effect found in foliage leaves there are clear patterns apparent in this data. Differences in vein density, leaf size and stomatal density between the two litter assemblages were small (Fig. 4-2). However, litter from the open canopy had slightly higher vein density than closed canopy litter ($P < 0.05$), although the difference in leaf size and density of stomata was marginal when comparing the two litter types.

The litter from open forest has slightly more veins for a given number of stomata than litter from the closed forest, although this difference was less than marginally significant ($P < 0.1$) and substantially smaller than the difference for leaves from foliage samples. This relationship remained almost the same after accounting for differences in leaf size. However, both litter types had low variance, small values of leaf size, and relatively high values of vein and stomatal density. In particular, the values are considerably closer to those for canopy (sun) leaves than those for sub-canopy (shade) leaves (Fig. 4-2).

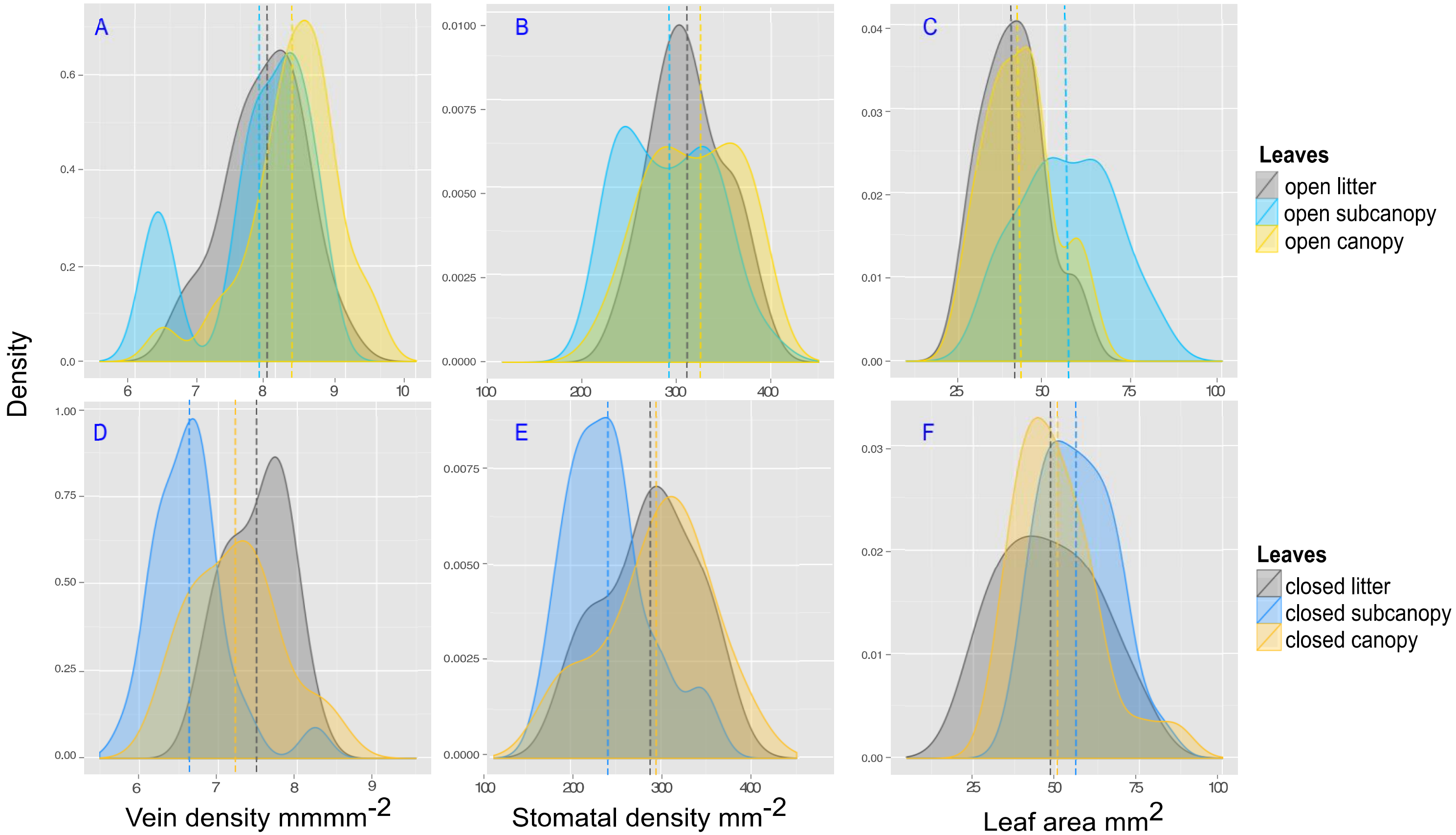

Figure 4-3-3 Vein density, stomatal density and leaf area probability curves showing canopy, subcanopy and litter from open and closed forest. Dashed lines represent the mean

4.4.4 Fossil samples

Leaf size and vein density did not vary significantly among fossils samples, although fossil assemblages differed in frequency of stomatal ($R^2 = 0.50$; $P < 0.01$). In particular, the fossils sample mh1 (6850 cal kyr BP) had 20% higher stomatal density, and the smallest leaves (26.39 ± 12 mm^2).

A visual comparison of the fossil and modern foliage data indicated that the values of vein density for sample mh1 fall within those of modern closed forest (Fig. 4-4). However, stomatal density for this sample is beyond modern values for the Lake Dobson area or any other reported values of stomatal density from modern leaves of *Nothofagus cunninghamii*.

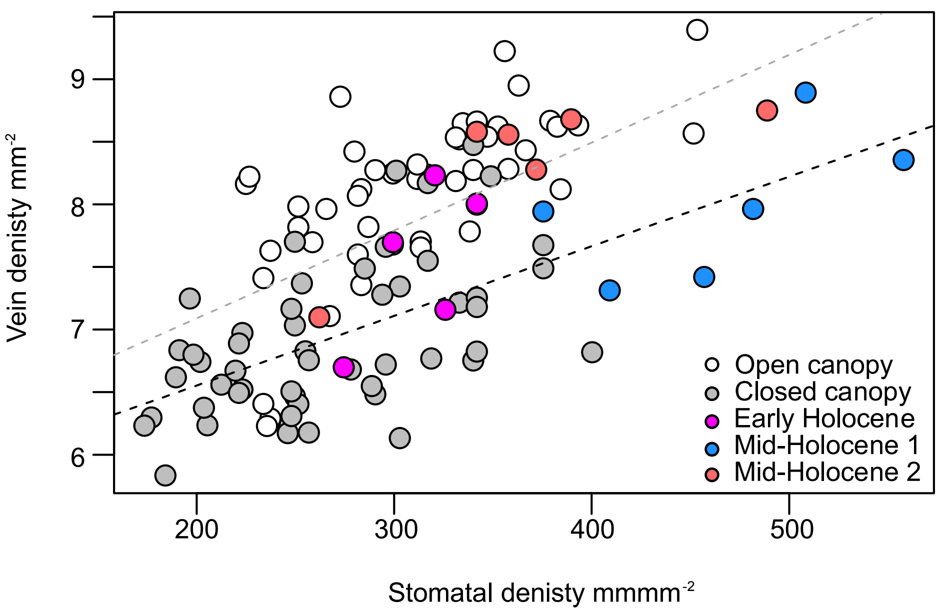

Figure 4-4 Leaf vein density and stomatal density values for open and closed canopy, early Holocene (~9350 cal kyr BP), mid-Holocene (mh1; 6850 cal kyr BP), and mid-Holocene.

4.5 Discussion

It is well known that within species, canopy leaves have more stomata and more veins that shade leaves, and are often smaller (e.g. Brodribb and Jordan 2011). This acclimation response is suggested to be adaptive, and primarily linked to the vertical decrease of light intensity through the tree canopy, and to the increase in evaporative demand (e.g. Niinemets 1998; Zwieniecki et al. 2004). There is also increasing evidence of tight coordination of these leaf parameters to maximise carbon gain (Carins Murphy et al. 2012), although few studies have explored whether this sun and shade leaf trait variation is reflected in comparable differences between open versus closed canopy forests and whether it can be used to reconstruct past forest structure.

This study provides important evidence of the differentiation in leaf parameters between open and closed forest stands in *Nothofagus cunninghamii*. In particular, results of this study indicate that canopy leaves bear higher density of stomata and veins, and smaller leaves compared to sub-canopy (shade leaves) as it has been reported in previous studies for *N. cunninghamii* and other vascular plants (Brodribb and Jordan 2011; Carins Murphy et al. 2012).

The overall significant relationship between vein density and forest structure, and in particular the higher leaf vein density for a given number of stomata in open canopy compared to closed forest in *N. cunninghamii* (Fig. 4-2), suggests that the theoretical coordination between tissues involved in the regulating the supply/loss of water from leaf extends to the whole tree. In particular, open forest leaves are exposed to higher levels of vertical solar radiation, exhibit higher rates of photosynthesis, and have much higher transpiration demand than shade leaves (Baldocchi and Amthor 2001). Thus, in this study the differential density of veins seen in open v. closed canopy trees it is likely a congruent response to differential water demands. This is further supported by the study of Brodribb and Jordan (2011) indicating lower hydraulic and stomatal conductance in association to lower vein density in shade leaves of *N. cunninghamii*.

Additionally, this study suggests that allowing for the effects of leaf size alongside with stomatal density in comparisons of vein density is potentially a useful tool for reconstructing the structure of the vegetation from fossil leaves. In particular, closed canopy leaves have lower vein densities relative to stomatal density compared to open canopy leaves especially, once differences in leaf size are taken into account. The fact that the relationship is dependent on leaf size and stomatal density is important because it means that canopy structure may be inferred from fossil leaves even when those leaves have undergone shrinkage in the process of fossilisation.

4.5.1 Litter and fossil leaf assemblages are biased toward sun-canopy leaves

Traditionally, litter studies elsewhere have focussed in the relationship between the litter production and the standing vegetation. However, several taphonomic factors can bias this relationship so that the interpretation of modern and fossil leaf assemblages is not straightforward (see Chapter 2). In particular, it was found that leaves from litter samples from the open *N. cunninghamii* forest had slightly more veins for a given number of stomata than those from closed forest, although this difference was non-significant and substantially smaller than the difference for leaves from foliage samples. Furthermore, both litter types exhibited low variance and relatively high values for both vein and stomatal density, although the values are considerably closer to those for canopy (sun) leaves than those for subcanopy (shade) leaves (Fig. 4-3). This higher upper to low canopy leaf representativity in the litter likely reflect higher rates of production of sun leaves because the net primary productivity (i.e. carbon gain through photosynthesis) of canopy leaves is higher than that of shade leaves, therefore it is likely that more canopy leaves are produced. Thus, the lack of response of both litter types to record canopy signature suggest a bias towards the incorporation of higher proportion of sun leaves in the litter due to higher sun to shade leaf rate of production. Other studies, however, have established that the higher representation of sun leaves in depositional settings is likely the result of differential dispersal abilities of sun and shade leaves, and higher likelihood of transport by wind (Spicer 1981; Spicer 1991).

Perhaps unsurprisingly, the fossils do not provide a compelling case for forest structure, because the small sample size. Despite this, a visual comparison of the fossil and modern foliage data indicated that vein density for the mid-Holocene sample (6850 cal kyr BP) fall within the values of vein and stomatal density values of the closed canopy forest (Fig. 4). However, the possibility of a closed canopy in the Lake Dobson area during the mid-Holocene is in disagreement with the composition of the vascular plant assemblages for this period (see Chapter 3) that suggest open and possibly low fire vegetation. However, wet and low light conditions are partially supported by the presence of some bryophyte species currently restricted to such environments (see Table 7-2 in Appendix 2; Fig. 3-3 and 3-4 in Chapter 3).

The stomatal density values for this sample are beyond modern values for the Lake Dobson area or any other reported values of stomatal density from modern leaves of *N. cunninghamii*. Furthermore, the fossils samples— and particularly for the mid-Holocene sample (6850 cal kyr BP)— had considerable smaller leaf sizes than leaves from either modern foliage or litter samples suggesting that leaves from these samples mainly represent sun leaves. This is further supported by a study conducted by Spicer (1981) indicating that leaf deposition in open-lake environments can be biased in size towards small sun leaves that often depart substantially from the overall size in the standing vegetation.

4.6 Conclusions

This study of leaf trait variation in *Nothofagus cunninghamii* demonstrated that leaf macrofossils have the potential be used to identify forest structure. Although further research is required to resolve the forest structure from litter, this approach represents an improvement on prior methods that directly employ vein density and have no capacity to allow for the effects of shrinkage or other taphonomic biases. Resolving the forest structure from litter is challenging, and it would require a very large sample to get enough shade leaves to create a significant signal. Even then, the application of this to the fossil record may be problematic because of the possibility of differential representation of canopy leaves over shade leaves because of better opportunity for transport to fossils sites.

This study also highlights the need for further research to understanding the modern relationship between leaf parameters and forest structure that is required to refine paleoclimatic interpretations based on leaf characteristics.

5 Chapter 5 – General discussion

5.1 Plant macrofossils as records of past local environments

Plant macrofossils have been rarely used for Lateglacial-Holocene vegetation reconstruction in southern temperate regions even though Northern Hemisphere studies have shown their potential value (Birks and Birks 2000; Valiranta et al. 2015). Typically, plant macrofossils can provide ecological and environmental information that is not often accessible by the analysis of fossil pollen —e.g. position and composition of past local vegetation at the treeline, location of glacial refugia, and information on the physiological response of species to climate and carbon dioxide (McElwain and Chaloner 1995; McElwain and Chaloner 1996; Tinner 2007; Traiser et al. 2005; Uhl et al. 2007). However, the validity of such analyses is largely dependent on understanding the taphonomic biases leading to the differential preservation of different species and plant organs in sediments. This thesis has therefore examined the use of plant macrofossils as a tool to assist Lateglacial-Holocene vegetation reconstructions in southern Australia.

5.2 Modern deposition of plant remains

Few of the available studies in Southern Hemisphere systems, and particularly Australia, have focused on understanding the inherent relationship between plant macrofossils incorporated in sediments, and the spatial distribution of different vegetation types, and abundance of different species. Most of these taphonomic studies have examined forest floor litter or accumulations of leaves on riverbanks and beds (Carpenter and Horwitz 1988; Steart et al. 2006; Steart et al. 2005), and only a handful have investigated lacustrine environments (Drake and Burrows 1980; Hill and Gibson 1986).

Lake Dobson in subalpine south-central Tasmania provides a well-constrained source vegetation area to depict factors affecting the modern deposition of plant remains in the lake sediments (Chapter 3). This study has demonstrated that the likelihood of a species becoming fossilised in systems similar to Lake Dobson is directly related to the distance of the plant community to site of deposition, and differential rate of leaf production among species. In particular, several lines of evidence suggest that the plant remains recorded in the sediments of Lake Dobson are likely to be almost exclusively derived from vegetation close to the lake (i.e. Lakeside and Eagle Tarn Creek vegetation). For instance, allochthonous elements from distant alpine communities are rare even though such vegetation occupies ~25% of the area of the hydraulic catchment of the lake. In contrast, common tree and shrubs in areas of vegetation close to the lake are well represented in the sediments. Thus, results presented in this study corroborate similar patterns found in other studies and systems (Birks 2001; 2007; Birks and Birks 1980; Gastaldo et al. 1996; McQueen 1969; Rich 1989; Rowell et al. 2001; Spicer and Wolfe 1987). Additional supporting evidence for the local origin of the plant material recorded is the presence of different plant organs (i.e. leaves, seeds, fruits and delicate floral structures). This feature is often considered to indicate parautochthony or autochthony, mainly because different plant parts may have differing transport potential (Ferguson 1985; Ferguson 2005; Gastaldo and Ferguson 1998; Gastaldo et al. 1996; Spicer 1989).

Further, results of this study suggest that differential leaf size and rate of production among species play a major role determining the final representation of species in sediments. In particular, temperate floras from Australia present high diversity of microphyllous and sclerophyllous evergreen species that produce higher amount of small leaves compared to main canopy trees. Thus, plant species presenting these traits would be expected to be strongly represented in depositional settings. For instance, *Eucalyptus coccifera*, the dominant canopy tree in the catchment of Lake Dobson is strongly underrepresented in modern sediments of the lake compared to its dominance in the catchment, and especially lakeside vegetation. This study provides evidence that *E. coccifera* and *E. subcrenulata* produce substantially less leaves per unit of ground vegetation than many shrub species from Ericaceae (Fig. 2-4 and Table 6-1 in Appendix 1). Thus, low rates of leaf production appear to be one important factor limiting the incorporation of leaves in sediments, and would help to explain the limited representation of the eucalypt leaves in fossil deposits in spite of the modern dominance of this group of plants in the Australian landscape. Taphonomic studies to date have provided additional evidence of the poor aerial dispersion and restricted preservation potential of *Eucalyptus* species (Carpenter and Horwitz 1988; Hill and Gibson 1986; Steart et al. 2005). It is plausible then, that a combination of taphonomic factors preclude the incorporation of *Eucalyptus* in depositional settings.

5.3 The assembly of treeline communities in south-central Tasmania

The plant macrofossil record examined in this study (Chapter 3) indicates that treeline plant communities in the area of Lake Dobson were assembled mainly from local glacial survivors following the microrefugial model of community assembly at the Lateglacial-Holocene transition. However, the delayed postglacial arrival of some important plant species, especially *Eucalyptus* around the early middle-Holocene boundary strongly supports later immigration from lowland areas.

The presence within the Lake Dobson area alpine conifer and shrubs at ca. 14 900 cal kyr BP before the Lateglacial-Holocene transition (Fig. 3-2) strongly suggests that alpine/subalpine plant communities assembled from local survivors shortly after deglaciation was completed ~16 000 cal BP (Mackintosh et al. 2006). This is further supported by a pollen-based vegetation reconstruction at Eagle Tarn, only 200 m from Lake Dobson (Fig. 3-1) that records the establishment of a proximal alpine community around the same time (12 800–12 000 14C years BP; Colhoun 1996). However, phylogeographic studies based on DNA provide evidence for the survival of a suite of species in areas that, according to pollen-based vegetation reconstructions, had environments inconsistent with the current environmental ranges of these species (Worth et al. 2009).

This *in situ* survival may indicate that relatively warm and sheltered microsites for the survival of woody plants may have been more common at high altitudes than previously thought. This is certainly consistent with that many chloroplast genotypes in *Nothofagus cunninghamii* are only found at high altitudes —and indeed are over-represented compared to genotypes at low altitude (Worth et al. 2009). Since the chloroplast evolves very slowly, this strongly suggests that this species survived in many high altitude locations, contrary to evidence from environmental niche modelling (Worth et al. 2014). The alternative explanation to local glacial survival, fast upward migration rate after the ice retreat, seems unlikely for at least the alpine conifers and *N. cunninghamii* which have very low dispersal abilities, infrequent production of seeds, and maturation time of ca. 100 years before plants can bear seeds (Cullen and Kirkpatrick 1988a; Hickey et al. 1982; Ogden 1978; Read and Hill 1985b).

In contrast to the evidence suggesting local glacial survival, the delayed postglacial arrival of *Eucalyptus* to the Lake Dobson area strongly support later immigration from lowland areas of refugia meaning that the modern configuration of the vegetation —i.e. *Eucalyptus* open woodlands— was not completed before the early middle-Holocene boundary ~8.1 cal. kyr BP (LD2 Fig. 3-2; 3-3 and 3-4). Indeed, it is distinctly possible that the lag time of arrival would be even later than suggested by pollen and our analyses, because there are now two species of *Eucalyptus* at Lake Dobson and these species were not differentiated in this analysis of fossils.

This result is in sharp contrast with pollen records in the Lake Dobson area and elsewhere at similar altitude sites in southern Tasmania. In particular, at Eagle Tarn (Fig. 3-1) pollen studies have indicated the arrival of *Eucalyptus* to subalpine areas around the Lateglacial-Holocene transition 10 000 ^{14}C yr BP at ca.11.5 kcal yrs. BP (10 000 14C yr BP; Colhoun 1996; Macphail 1979; Markgraf et al. 1986). It is credible that the discrepancies between the two record may reflect taphonomic bias in pollen representation. In particular, it is well known that uphill wind transport of tree pollen grains from plant communities at low altitudes can lead to high abundance of these pollen types in treeless alpine Lateglacial environments (Barnekow, 1999; Birks and Birks, 2008; Birks, 2003; Birks and Birks, 2000; Wick et al., 2003). Although the record of *Eucalyptus* at Lake Dobson mainly consist of leaf fragments, its absence in Lateglacial-early Holocene sediments cannot be explained by low preservation potential or misidentification as remains are consistently present in the record after 8.1 cal kyr BP and are relatively abundant in recent assemblages (Chapter 2). Importantly, the lag-time in migration recorded in the macrofossil record is consistent with the low dispersal capabilities typical of *Eucalyptus* species (Jordan 2003; Potts 1990; Shaw et al. 1984). This is further supported by molecular evidence evidencing the survival of eucalypts in multiple lowland glacial refugia (McKinnon et al. 2004; Nevill et al. 2008; Nevill et al. 2010), and subsequent expansion into formerly glaciated areas following the ice retreat (Byrne, 2008; McKinnon et al., 2004). Thus, it is likely that the lag in migration of *Eucalyptus* may have been constrained by the distance from lowland areas of refugia, possibly with a contribution of competition from the existing species in the area. Furthermore, the strong lag migration of *Eucalyptus* evidenced in the macrofossil record was not constrained by lack of fire or unsuitable climates, because charcoal is recorded throughout the sediment profile, and temperatures became suitable at least 4000 years before the genus appears in the record (Fig. 3-2).

5.4 Reconstructing forest from fossil *N. cunninghamii* leaves

The potential for leaf macrofossils to identify forest structure using contemporary leaves of the evergreen tree species *Nothofagus cunninghamii* explored in Chapter 4 indicates that this species is a good candidate for such investigations. This is mainly because *Nothofagus cunninghamii* is known to show substantial leaf anatomical variation in response to sun and shade (Brodribb and Jordan 2011; Hovenden and Vander Schoor 2006), and is an important component of modern and fossil floras in Tasmania and other southern temperate regions (Hill and Jordan 1993; Hill et al. 2015; Read et al. 2010).

A principal finding of this study is the strong differentiation in leaf parameters between open and closed forest stands of *N. cunninghamii*. Importantly, this study suggests that open canopy leaves present higher density of veins for a given number of stomata compared to closed forest (Fig. 4-2). This differentiation has also been observed among sun and shade leaves, and it argues for the coordination of tissues involved in the regulation of water transport and demand present in the leaf extends to the whole tree. In particular, open forest leaves are exposed to higher levels of solar radiation, present much higher photosynthetic yields, and consequently have higher rates of transpiration than shade leaves that require higher vein density for water transport. This finding is further supported by the study of Brodribb and Jordan (2011) indicating lower hydraulic and stomatal conductance in association to lower vein density in shade leaves of *N. cunninghamii*.

Additionally, the differential strong coordination between veins and stomata observed for the two canopy types suggest that allowing for the effects of leaf size alongside the with stomatal density in comparisons of vein density is potentially a useful tool for reconstructing the structure of past vegetation from fossil leaves. The fact that the relationship is dependent on leaf size and stomatal density is important because it means that canopy structure may be inferred from fossil leaves even when those leaves have undergone shrinkage in the process of fossilisation.

It is well known that several taphonomic factors can bias the relationship between the standing vegetation, and the production of litter so that the interpretation of modern and fossil leaf assemblages is not straightforward (see Chapter 2). In particular, this study has revealed small differences in leaf parameters between the two litter types, and differences substantially smaller than for leaves from foliage samples. Furthermore, the two litter types presented high representation of canopy leaves with relatively high stomatal and vein density (Fig. 4-3). Thus, the lack of response of both litter types to record canopy signature suggest a bias towards the incorporation of higher proportion of sun leaves in the litter due to higher sun to shade leaf rate of production. One possible way to resolve forest structure from the litter would involve a much extensive sampling to get a higher representation of shade leaves to create a significant signal. However, the application of this methodology to the fossil record may be still problematic because of the possibility of differential representation of canopy leaves over shade leaves due to better opportunity for transport to depositional settings (Spicer 1981). The fossils do not provide a compelling case for forest structure, because the small sample size. Additionally, all samples —and especially mid-Holocene sample (6850 cal kyr BP)— have considerable smaller leaf sizes than leaves from either modern foliage or litter samples suggesting that leaves from these samples mainly represent sun leaves. This is further supported by a study conducted by Spicer (1981) indicating that leaf deposition in open-lake environments can be biased in size towards small sun leaves that often depart substantially from the overall size in the standing vegetation mainly because differential dispersal abilities of sun and shade leaves, and higher likelihood of transport by wind (Spicer 1981; Spicer 1991).

6 Appendix 1 – to Chapter 2

Composition of standing vegetation and litter

Lakeside vegetation

This area of vegetation includes the standing vegetation immediately surrounding Lake Dobson (Fig. 2-1), and typically represents *Eucalyptus* woodland with a dense understory of heath species. This unit of vegetation is the major component of the subalpine vegetation below the treeline and around the lake. It is dominated by *Eucalyptus coccifera* and *E. subcrenulata* interspersed with isolated trees or small groups of the evergreen montane rainforest species *Nothofagus cunninghamii* (Nothofagaceae) or the endemic conifer *Athrotaxis cupressoides* (Cupressaceae).

Fifty-two plant species within 23 different families were recorded in this area of vegetation. These included 33 species of shrubs, four trees, nine monocotyledonous herbs, four dicotyledonous herbs, and two species of ferns. Common tree and shrub species (Fig. 2-4) typically belong to the families Myrtaceae, Ericaceae, and Proteaceae with frequent species and abundance values including *E. coccifera* (51%), *Richea scoparia* (28%), *E. subcrenulata* (27%), *Leptospermum lanigerum* (13%) and the conifers, *Athrotaxis cupressoides* (13%), and *Pherosphaera hookeriana* (8%). Herbs species, monocotyledonous and dicotyledonous, such as those members of the families Cyperaceae, Asteliaceae, Restionaceae, Asteraceae and Haloragaceae were rare in this area of vegetation representing respectively 4% of the total cover abundance of species.

Golden Stairs Creek vegetation

The Golden Stairs Creek vegetation extends from the west side of Lake Dobson up to Mawson Plateau along the Golden Stairs Creek, one of the main inflowing streams to the lake (Fig. 2-1). In this area of vegetation, 45 species from fifteen different families were recorded. The most abundant taxa were tree and shrub species from the Ericaceae (28%), Proteaceae (22%), and Myrtaceae (18%) with dominant species such as, *Orites revolutus* (16%), *Richea sprengelioides* (9%), *Eucalyptus coccifera* (8%), *N. cunninghamii* (6%), *Leptospermum rupestre* (6%), *Epacris serpyllifolia* (4%), and *Eucalyptus subcrenulata* (2%). Five species of conifers were found accounting for 8% of total representation (Fig. 2-4). The most common monocotyledons were *Astelia alpina* (Asteliaceae) and *Gahnia grandis* (Cyperaceae).

Eagle Tarn Creek vegetation

The area of vegetation along Eagle Tarn Creek typically represents a stand of montane rain forest. It extends toward the north part of lake along Eagle Tarn Creek (Fig. 2-1). It presented the highest richness of species among all areas of vegetation with 55 species within 20 families. Dominant species are the conifers *Athrotaxis cupressoides* and *Pherosphaera hookeriana* accounting together for 43% of relative abundance. Other dominant species were the rainforest species *Nothofagus cunninghamii* (18%), alongside with *Richea pandanifolia* (10%), *Richea scoparia* (9%), and *Eucalyptus coccifera* (8%), among others (2-4).

Upper catchment vegetation

The upland vegetation area (Fig. 2-1) represents typical alpine vegetation of the upper catchment. It was, without including herbs, the area of lowest species richness with only 39 species within twelve families. Most commonly represented families were Myrtaceae 47%, Ericaceae 28%, Proteaceae 16%, and Nothofagaceae 11%. Three species of dwarf conifer species —*Diselma archeri*, *Microcachrys tetragona*, and *Pherosphaera hookeriana*— were present in this area of vegetation, although their relative abundance was low (1%). Dominant species in this area of vegetation were *Eucalyptus coccifera* 26%, *Nothofagus cunninghamii* 11%, and *Richea pandanifolia, Eucalyptus subcrenulata* and *Leptospermum lanigerum* with 7% of total representation (2-4).

Litter samples

Twenty-two tree and shrub species were identified in the litter samples representing ~ 60% of the total number of species recorded in the lakeside vegetation (herbs and ferns not included). Five species present in the litter samples were completely absent from the macrofossil assemblages: *Telopea truncata*, *Bellendena montana* and *Lomatia polymorpha* from Proteaceae, *Baeckea gunniana* from Myrtaceae, and *Pentachondra pumila* from Ericaceae.

Table 6-1 Common species represented in the sediments of Lake Dobson and areas of vegetation. Numbers of subfossil leaves, values of leaf size, per leaf area representation and number of leaves include rank order values in brackets. *Conifer species.

Species (life-form)	# Subfossil leaves	Mean leaf size (mm^2)	Per leaf area representation (mm^2)	LMA ($g\ m^{-2}$)	# Leaves per species
E. serpyllifolia (shrub)	12205 (1)	4 (20)	54056 (4)	157(16)	791857 (1)
L. juniperina (shrub)	405 (11)	8 (18)	3148 (15)	217(10)	762652 (2)
T. thymifolia (shrub)	11 (20)	6 (19)	70 (20)	169(15)	596682 (3)
L. lanigerum (shrub)	2400 (2)	18 (13)	42718 (5)	136(19)	351825 (4)
B. rubioides (shrub)	1748 (4)	9 (17)	16182 (8)	102(20)	294381 (5)
P. hookeriana (shrub)*	836 (7)	11 (15)	9478 (11)	504(2)	256198 (6)
C. straminea (shrub)	36 (17)	36 (8)	1289 (19)	195(12)	202729 (7)
T. cunninghamii (shrub)	481 (10)	13 (16)	6233 (13)	149(17)	191380 (8)
C. nitida (shrub)	170 (12)	16 (14)	2717 (17)	193(13)	176449 (9)
O. revolutus (shrub)	714 (8)	22 (12)	15501 (9)	425(5)	164506 (10)
S. incarnata (shrub)	79 (16)	31 (10)	2446 (18)	140(18)	108579 (11)
O. pinifolia (shrub)	128 (14)	38 (7)	4837 (14)	457(4)	97585 (12)
O. acicularis (shrub)	574 (9)	35 (9)	20310 (7)	493(3)	86485 (13)
R. scoparia (shrub)	159 (13)	59 (5)	9322 (12)	205(11)	77597 (14)
A. cupressoides (tree)*	1955 (3)	31(11)	61323 (3)	841(1)	76132 (15)
N. cunninghamii (tree)	1352 (5)	569 (6)	769346 (2)	301(6)	66807 (16)
T. lanceolata (shrub)	21 (18)	140 (4)	2933 (16)	189(14)	38843 (17)
O. diversifolius (shrub)	103 (15)	203 (3)	20901 (6)	277(8)	12150 (18)
E. coccifera (tree)	939 (6)	897(2)	842456 (1)	246(9)	2130 (19)
E. subcrenulata (tree)	14 (19)	930 (1)	13019 (10)	302(7)	1655 (20)

7 Appendix 2 - to Chapter 3

Table 7-1 Radiocarbon dates from Lake Dobson Mt. Field National Park, Tasmania. * Samples were analysed at the UCI Keck Carbon Cycle AMS Program University of California, Irvine, USA. **Calibration was run with CLAM 2.2 (Blaauw 2010) using the Southern Hemisphere curve SHCal13 with an offset of 40 years (Hogg et al. 2013).

Sample ID	Depth cm	Sample description	^{14}C yr BP ± SD*	Cal yr BP **
UCIAMS-76880	118	Bark, Eucalyptus leaf	955 ± 20	838
UCIAMS-76881	206	*Eucalyptus* leaf	1795 ± 20	1661
UCIAMS-76882	285	Bark, small leaves	2555 ± 20	2591
UCIAMS-76883	393	Leaf fragments, stems	3750 ± 25	4009
UCIAMS-76884	530	Woody fragments	5790 ± 20	6690
UCIAMS-76885	599	Woody fragments	8235 ± 25	8900
UCIAMS-76886	697	Leaf, woody fragments	9795 ± 35	11334
UCIAMS-76887	780	*Microcachrys* fragments	12035 ± 35	13568
UCIAMS-76888	825	*Microcachrys* fragments	12240 ± 30	14188
UCIAMS-76889	928	*Microcachrys* fragments	12555 ± 35	14845

Table 7-2 Plant macrofossil species recorded in the sediments of Lake Dobson. Plant species are grouped by clade and family and separated by foliar and reproductive organs. Taxonomic authorities and main habitat descriptions for modern species are given.

Group-family	Species	No. of foliar organs	No. of reproductive organs	Modern habitat
Gymnosperms-conifers				
Cupressaceae	*Athrotaxis cupressoides* D.Don	349	-	Open alpine/subalpine vegetation, although can also occurs as rainforest species. In fire-protected areas.
	Athrotaxis laxifolia Hook.	24	1 (female cone)	Common in alpine areas.
Podocarpaceae	*Diselma archeri* Hook.f.	596	-	In high rainfall alpine/subalpine areas on alpine coniferous heath and montane rainforest.
	Phyllocladus aspleniifolius (Labill.) Hook.f.	4	-	Rainforest
	Pherosphaera hookeriana W.Archer	69	-	In fire protected alpine/subalpine areas on coniferous heath and montane rainforest.

	Microcachrys tetragona (Hooker) Hook.f.	273	-	In alpine and open subalpine fire-protected areas often in rocky soils.
	Podocarpus lawrencei Hook.f.	2	-	Mostly in alpine/subalpine areas in relatively fire-free areas, and boulder fields.
Angiosperms-dicotyledonous			-	
Cunoniaceae	*Bauera rubioides* Andrews	49		It grows in wet open areas in a range of habitats.
Ericaceae	*Cyathodes straminea* R.Br.	2	-	Mostly in subalpine areas.
	Epacris serpyllifolia R.Br.	494	174 (floral bracts)	
	Leptecophylla juniperina (J.R.Forst. & G.Forst.) C.M.Weiller	17	-	It grows in a wide range of habitats from sea level to alpine.
	Montitega dealbata (R.Br.) C.M.Weiller	7	-	Alpine areas.
	Pentachondra pumila R.Br.	-	1 (flower)	Alpine areas.
	Planocarpa petiolaris (DC.) C.M.Weiller	3	-	Alpine/subalpine dolerite mountains.
	Richea scoparia Hook.f.	55	-	Alpine/subalpine areas.

	Richea sprengelioides (R.Br.) F.Muell.	13	-	
	Sprengelia incarnata Sm.	13	-	Widespread shrub from low to high altitudes in wet peaty places.
	Trochocarpa cunninghamii (DC.) W.M.Curtis	8	-	Subalpine or rainforest shrub.
	Trochocarpa R.Br.	-	7 (seeds)	*T. gunnii*: common in alpine and subalpine areas. *T. cunninghamii*: subalpine or rainforest.
Haloragaceae	*Gonocarpus montanus* (Hook.f.) Orchard	-	1	Common in alpine/subalpine areas.
Myrtaceae	*Baeckea gunniana* Schauer ex Walp.	2	-	Alpine/subalpine species.
	Eucalyptus coccifera Hook.f.	244	3 (capsules)	High altitude species, usually forming the treeline.
	Leptospermum lanigerum (Aiton) Sm.	7	-	A wide variety of habitats, often waterlogged.
	Leptospermum rupestre Hook.f.	25	-	Alpine and subalpine shrub.
	Myrtaceae Juss. (possibly *Eucalyptus*)	-	15 (seeds)	
Nothofagaceae	*Nothofagus cunninghamii* (Hook.) Oerst.	179	2 (seeds)	Cool temperate and montane rainforest.
	Nothofagus gunnii (Hook.f.) Oerst.	4	-	
Proteaceae	*Orites acicularis* (R.Br.) Roem. & Schult.	69	-	Common alpine/subalpine shrub.

	Orites revolutus R.Br.	14	-	Very common alpine shrub.
Rubiaceae	*Coprosma nitida* Hook.f.	13	-	Common in subalpine areas.
Winteraceae	Tasmannia lanceolata (Poir.) A.C.Sm.	3	2 (seeds)	From wet forest to alpine areas.
Angiosperms-monocotyledonous				
Cyperaceae	*Gahnia grandis* (Labill.) S.T.Blake	-	2 (seeds)	In wet forests, especially after fire.
Pteridophyta - ferns				
Gleicheniaceae	*Gleichenia alpina* R.Br.	9 (trichomes)	-	Boggy alpine and subalpine areas.
Blechnaceae	*Blechnum penna-marina* (Poir.) Kuhn	3 (trichomes)	-	Common in damp places in alpine/subalpine areas.
Bryophytes-mosses				
Acrocladiaceae	*Acrocladium chlamydophyllum* (Hook.f. & Wilson) Müll. Hal. & Broth.	68	-	Wet forest usually on tree trunks and bases, and terrestrial in disturbed grassy areas.
Andreaeaceae	*Andreaea australis* Mitt.	32	-	Alpine/subalpine *Eucalyptus* woodlands, grassland, heaths and herbfields on rock surfaces, very rarely on the ground.
	Andreaea mutabilis Hook.f. & Wilson	16	-	Alpine/subalpine *Eucalyptus* woodlands, heaths, grasslands, shrublands, on wet to dry outcrops and boulders.
	Andreaea subulata Harv.	8	-	*Eucalyptus* and *Nothofagus* forest and woodland grasslands with heathy patches, often at the edge of watercourses on rock.

Bartramiaceae	*Bartramia mossmaniana* Müll. Hal.	39	-	Alpine/subalpine rock crevices, and damp forests on wet rocks and soils, near streams.
	Breutelia pendula (Sm.) Mitt.	1127	-	Alpine bogs and streams, wet habitats in montane regions. In Australia, it is found in very moist conditions at higher elevations.
	Breutelia affinis (Hook.) Mitt.	9	-	Rocks and soil in permanently or occasionally moist conditions.
Brachytheciaceae	*Brachythecium rutabulum* (Hedw.) Schimp.	11	-	Forests ground, logs, tree trunks and shrub stems, or on rocks, in moist or shaded habitats, on the banks of creeks and rivers.
	Brachythecium paradoxum (Hook.f. & Wilson) A.Jaeger	13	-	Montane forests, alpine/subalpine woodlands, grassland and heathland on ground, rocks, tree trunks or tree stumps.
Bryaceae	*Bryum mucronatum* Mitt.	6	-	
	Bryum harriottii R.Br.bis	8	-	
	Gemmabryum laevigatum Hook.f. & Wilson	6	-	
	Bryum Hedw.	182	-	
Catagoniaceae	*Catagonium nitens* (Brid.) Cardot	2	-	Damp soil or rocks in wet sclerophyll forest or in drier habitats such grasslands in upland areas.
Daltoniaceae	*Distichophyllum microcarpum* (Hedw.) Mitt.	298	-	Rock or rarely logs in shaded wet sclerophyll forest or rainforests
Dicranaceae	*Dicranoloma billardieri* (Brid.) Paris	22	-	Various forest types from dry sclerophyll to temperate rainforests, and in open alpine vegetation above the treeline.

	Dicranoloma dicarpum (Nees) Paris	2	-	Various forest types from wet. Sclerophyll to temperate rainforest, rare in dry forest. It forms as loose turfs on rocks, logs, and trees.
	Dicranoloma robustum (Hook.f. & Wilson) Paris	2	-	Wet forest, rainforest, and alpine moorland It grows as loose turfs on rocks, logs and trees.
	Dicranoloma platycaulon Dixon	12	-	Temperate rainforest. In Australia restricted to *Nothofagus cunninghamii* bark high up in the stem.
	Dicranoloma spp. (Renauld) Renauld	163	-	
	Dicranella cardotii (R.Br.bis) Dixon	6	-	Wet soil or soil over rock, usually near streams.
	Campylopodium medium (Duby) Giese & J.P.Frahm	20		Bare soil.
Ditrichaceae	*Ditrichum cylindricarpum* (Müll.Hal.) F.Muell.	10	-	
	Ditrichum difficile (Duby) M.Fleisch.	9	-	Wet forests, and alpine/subalpine areas on soil and earth banks.
Fissidentaceae	*Fissidens rigidulus* Hook.f. & Wilson	1898	-	Rocks in fast-flowing water.
	Fissidens pallidus Hook.f. & Wilson			Dump bare soils, especially clay banks
	Fissidens berteroi (Mont.) Müll.Hal.	37	-	Running water attached to rocks or soil but floating.
Funariaceae	*Entosthodon radians* (Hedw.) Müll.Hal.	18	-	Mostly in bare soils in dry habitats
Grimmiaceae	*Racomitrium crispulum* (Hook.f. & Wilson) Hook.f. & Wilson	56	-	Exposed wet or dry siliceous rocks.
	Grimmia trichophylla Grev.	2	-	Exposed siliceous rocks, common mosses of rocks and boulders.

Hypnaceae	*Hypnum chrysogaster* Müll.Hal.	25	-	Grows on tree trunks and decaying wood in forest, rarely on the ground; from lowlands up to c. 1000 m.
	Hypnum cupressiforme Hedw.	6	-	Open and forested habitats on various substrata. Cosmopolitan in temperate and colder regions.
	Hypnum sp Hedw.	131	-	
Hypnodendraceae	*Hypnodendron comosum* (Labill.) Mitt.	117	-	Permanently moist habitats, soils and rock in dump to wet forests
	Hypopterygium didictyon Müll.Hal.	10	-	Cool temperate rainforest, tree-fern gullies and other wet, sheltered places in wet and damp forests.
Lembophyllaceae	*Camptochaete arbuscula* (Sm.) Reichardt	12	-	Cool temperate rainforest (300-1000 m), fern gullies, and other dam places On tree bases, rocks and soil.
	Weymouthia Broth.	55	-	Epiphyte in wet and rain forest, usually on branches, and trunks.
Leptostomaceae	*Leptostomum inclinans* R.Br.	10	-	Epiphytic species often high in tree-trunks *Eucalyptus* and *Nothofagus* and in crevices of granitic rocks.
Leucobryaceae	*Campylopus* spp. (R.Br.) Hook.f & Wilson	52	-	*C. bicolor*/*C. clavatus*. Terrestrial or on rocks. Normally in sites periodically inundated in otherwise dry vegetation types.
Neckeraceae	*Thamnobryum pumilum* (Hook.f. & Wilson) Nieuwl.	38	-	It grows on rocks in streams or watercourses in wet sclerophyll forest.

Orthodontiaceae	*Leptotheca gaudichaudii* Schwägr.	160	-	In wet sclerophyll forest. Frequently found on old tree trunks, dead timber, tree ferns, rocks, and soil.
Orthotrichaceae	*Zygodon hookeri* Hampe	5	-	Occurs on bark and twigs in wet sclerophyll forest, most commonly as an epiphyte (often on *Nothofagus*) and occasionally on rocks.
	Zygodon intermedius Bruch & Schimp.	19		Epiphytic on a wide range of trees and shrubs, but also found on rock. It tolerates wide range of humidity, although it is absent from the driest habitats.
	Orthotrichum rupestre Schleich. ex Schwägr.	4	-	Cosmopolitan moss. It grows from lowland to montane environments mainly on rocks and boulders, occasionally bark, and dry to moist.
	Orthotrichum tasmanicum Hook.f. & Wilson	2	-	Bark or twigs on the margins of wet sclerophyll forest.
Pleurophascaceae	*Pleurophascum grandiglobum* Lindb.	2	-	Bogs and streams. Completely aquatic, or partly under water
Polytrichacea	*Polytrichum juniperinum* Hedw.	5	-	A common species of dry, exposed, acidic habitats. Frequently occurring as a pioneer on recently disturbed or burnt, acidic soils.
Pottiaceae	*Tortula* Hedw.	1	-	Exposed siliceous rocks.
Pylaisiadelphaceae	*Wijkia extenuata* (Brid.) H.A.Crum	70	-	Very common in moist situations, from damp forest to rainforest. Usually found on fallen logs or on the bases or trunks of trees, rarely on rock or on soil.

Ptychomniaceae	*Ptychomnion aciculare* (Brid.) Mitt.	26	-	Common in damp, wet environments and rainforest, on rotting logs, tree trunks, and sometime soils. In very wet situation, it occurs as an understory epiphyte.
	Hampeella alaris (Dixon & Sainsbury) Sainsbury	11	-	Grows in cool temperate rainforest. Often found growing as epiphyte on *Nothofagus cunninghamii*, and other rainforest species.
Rhacarpaceae	*Rhacocarpus purpurascens* (Brid.) Paris	51	-	Vertical faces of granite rock in drier forest. In alpine areas, it is common on granite where water runs off.
Rhizogoniaceae	*Rhizogonium novae-hollandiae* (Brid.) Brid.	36	-	Grows on wood and tree ferns in moist habitats.
	Pyrrhobryum Mitt.	67	-	*P. minoides* grows on rock and soil, rarely on wood. *P. parramattense* occurs in very moist environments, commonly on wood.
Seligeriaceae	*Blindia robusta* Hampe	5	-	Alpine areas in soak and pools.
Sphagnaceae	*Sphagnum* L.	539	-	Alpine bogs. *S. cristatum*: Mainly subalpine. *S. australe* in lowland to subalpine, usually well-drained habitats.
Thuidiaceae	*Thuidiopsis furfurosa* (Hook.f. & Wilson) M.Fleisch.	305	-	Mostly in terrestrial moist environments. In swamps, subalpine grasslands, and on rocks or banks near forest streams, occasionally forming large patches in grassland and light bush.
Hepatophyta-liverworts				
Cephaloziellaceae	*Cephaloziella exiliflora* (Taylor) Douin	3	-	Mainly on the surface of burnt wood.

Geocalycaceae	*Leptoscyphus* Mitt.	146	1	Leafy liverwort from cool temperate rainforests.

Table 7-3 Results of the parsimonious CCA performed on plant macrofossil abundance and forward selected environmental variables

Explanatory variables	**CCA axes**		
Biplot scores for environmental variables			
	1	2	3
Composite temperature	-0.9104	-0.3639	-0.1950
CO_2	0.9870	-0.1412	0.0779
Charcoal influx	0.1636	-0.2900	0.9429
Summary statistics for ordination axes			
Eigenvalue	0.3152	0.06777	0.04416
Proportion explained	0.7379	0.15867	0.10339
Species-environment correlation	0.9427	0.6718	0.6762
Total inertia	2.6613		
Constrained inertia	16%		
Unconstrained inertia	84%		

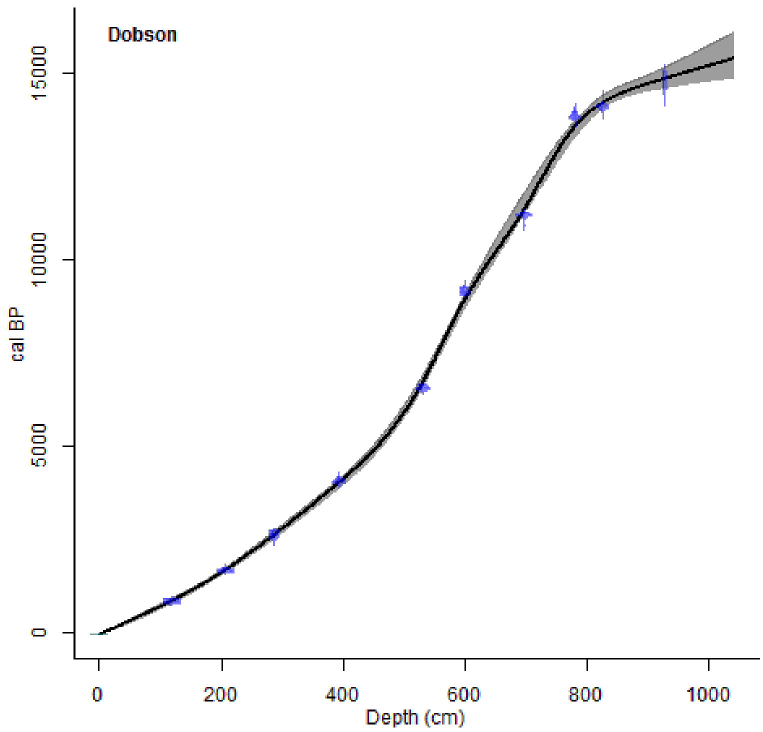

Figure 7-1 Age-depth model for Lake Dobson (Rees et al. 2015) derived from 10 radiocarbon dates. The model was developed using CLAM 2.2 (Blaauw 2010), and the Southern Hemisphere curve SHCal13 (Hogg et al. 2013). Blue bars represent the highest probability density of each date while the grey fill represents the 95% confidence intervals of the calibration range.

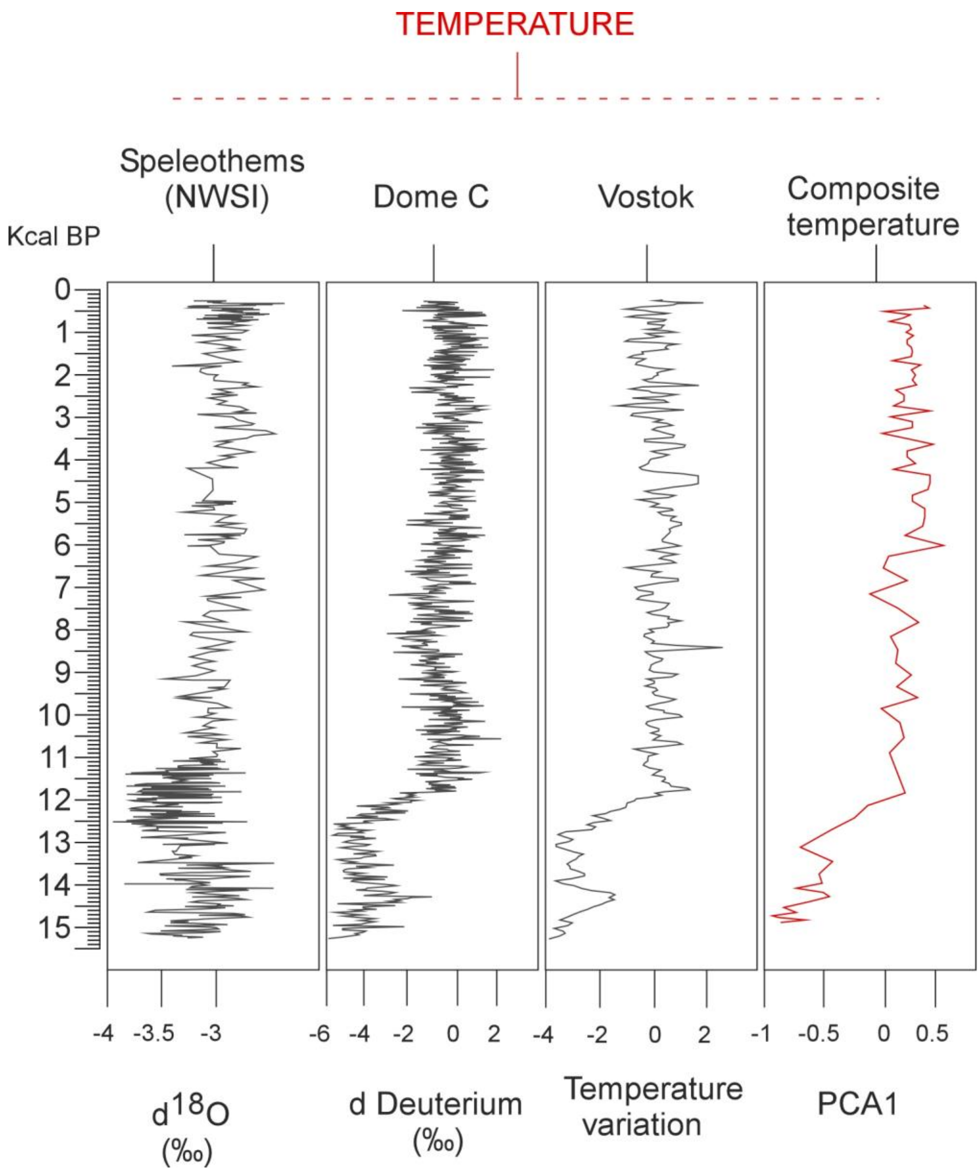

Figure 7-2 Comparison of Southern Hemisphere temperature reconstructions, and composite temperature curve (PCA axis 1) derived by principal component analysis.

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